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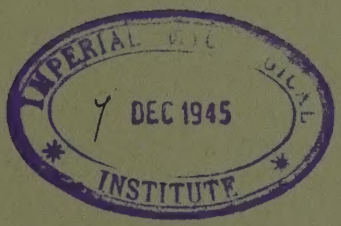

PROPOSED FUTURE
CONTENTS ON REAR COVER

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RADIATION AND PLANT RESPIRATION

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CONTENTS

INTRODUCTION

Over a period of nearly a century the many investigations which have dealt with the influence of radiation upon respiration and fermentation of plants have given rise to a mass of contradictory and confusing data. The situation is doubtless to be attributed, in large part, to the inadequate facilities for control and measurement of environmental factors, such as temperature and radiation, which have generally been available. In other cases the analytical methods used have not been sufficiently precise for the determination of small effects. In addition, there is evidence in some work that apparently minor variations in the biological materials and experimental conditions employed may have greatly influenced the results obtained.

The present review is little more than an attempt to assemble the scattered literature bearing on the subject of radiation and plant respiration. An extended theoretical discussion of the mechanisms involved would not seem to be justified by the experimental evidence so far available, nor will it be feasible to give more than passing mention to many collateral fields of knowledge which eventually may prove to contribute to an explanation of these mechanisms. Consideration of photodynamic effects and of the reversal of chemical inhibition of respiration by light has not been included. For previous reviews of various aspects of the literature, the reader is referred to (49, 61, 156, 179, 245, 326).

The influence of radiation upon plant respiration is of interest not alone in its bearing on our understanding of respiration itself and of the effects of radiation upon plants, but also because of the importance of evaluating the rôle of this factor in experiments dealing with other aspects of respiration or with photosynthesis.

It will not be attempted here to formulate a definition of respiration from the standpoint of the vital economy of the organism. Indeed, with our present crude experimental technics it is often impossible to distinguish respiration from other processes which may be functionally quite unrelated to it. Theoretically, respiration may be measured by changes in the composition of the respiring material or by changes in the environment. Actually, the latter methods (usually employing alterations in oxygen and/or carbon dioxide content of the environment) are far more practicable and

convenient and have been used almost without exception in the experiments herein reviewed.

In the following discussion the literature has been arranged primarily with respect to the kinds of radiation and the types of biological materials studied, rather than in chronological sequence. As a matter of convenience a quite arbitrary classification has been adopted.

EFFECTS OF VISIBLE RADIATION ON RESPIRATION

Since the overall respiratory reaction is, generally speaking, just the reverse of the photosynthetic reaction, direct evidence of alterations in respiration, due to light, can be obtained only with material naturally incapable of photosynthesis or in which photosynthesis is suppressed by suitable experimental treatment. Indirect evidence along a number of lines may be derived, however, from photosynthetic material.

It should be borne in mind that in many of the studies to be discussed in this section it is probable, or even certain, that infra-red, and in some cases also ultra-violet, was included in the radiation employed. The sources of radiation and types of filters used will be indicated wherever such information is available.

Non-Chlorophyllous Plants and Tissues

Fungi. Microbiological literature contains many references (*e.g.*, 46) to the effects of radiation upon respiration and fermentation of various bacteria, yeasts and molds. Only that portion of this literature in which the effects on the metabolic processes can be distinguished, to some degree at least, from the more general effects on growth and reproduction, will be considered here.

One of the earliest reports is that of Schutzenberger and Quinquaud[1] who in 1873 measured the oxygen consumption of beer yeast suspensions. No differences in rate were found in darkness, in diffuse light, or in direct sunlight. No data on temperature were included. More recently, the rate of aerobic oxygen consumption or of anaerobic carbon dioxide production of baker's yeast in glucose solution was found to be substantially the same in darkness and in light of fairly high intensity (75-watt tungsten filament lamp at 4 cm. distance) (314). According to Tang, exposure of *Saccharo-*

[1] Since every author and article mentioned in the text is cited in the bibliography, reference numbers are given only when necessary to avoid confusion.

myces wanching to the visible portion of the radiation from a quartz mercury arc did not affect the subsequent rate of oxygen consumption in darkness. Similar results were reported by Schneider (263).

Van der Paauw found a 20% increase in oxygen consumption of *Saccharomyces vordermanii* during illumination, presumably by a 150-watt lamp at about 14 centimeters distance, filtered through eight to nine centimeters of water.

Dumas stated that yeast fermentation proceeded more slowly in darkness than in light. According to Lubimenko and Froloff-Bagreief, exposure of raisin must, inoculated with yeast, to daylight over a long period of time resulted in an approximately 20% decrease in the amount of carbon dioxide produced, as compared with the dark control. The decreases in amount of sugar fermented and in amount of alcohol formed in light were somewhat less.

Von Euler and Laurin reported that a 30-minute exposure to sunlight produced a 5% decrease in the fermentation capacity of yeast. Polarized light was stated to stimulate fermentation of sucrose by *Saccharomyces cerevisiae* (182). Guerrini, who measured the fermentation of glucose by yeast, reported a greater rate of carbon dioxide production in light than in darkness (114–116, 118). The order of effectiveness of the light was stated to be red > yellow > green > blue > white, although the intensities do not appear to have been equalized in the various spectral regions.

Irradiation by the wavelength band 5,000–6,500 Å was reported to increase the fermentation rate of yeast (111). The stimulation persisted for some time after the irradiation had been discontinued. Murakami exposed koji-extract cultures of *Saccharomyces cerevisiae* and *S. ellipsoideus* to various wavelength bands of visible plus infrared radiation (of unequalized intensities) during a 96-hour incubation period. Determinations of alcohol, aldehyde, acetal, ester and acids showed small and irregular differences, of which the significance is rather doubtful, especially as only a single experiment was performed (199; see also 198, 200).

Rubenstein, using the Warburg technic, measured oxygen consumption by *Sarcina lutea.* Under starvation conditions at 37° C., the initial respiration rate was as much as five times as great in darkness as in Mazda radiation, filtered through water and glass, of

about 556 meter-candles intensity. By the end of 48 to 72 hours the oxygen uptake fell to practically nil; the total quantity of oxygen absorbed was approximately the same in the irradiated and in the dark cultures. A quite different result was found at 20°, at which temperature the rate of oxygen consumption was increased by illumination. At about 30° the respiration rate was the same in light and in darkness. At 37° the rate was decreased by illumination, also in the presence of low concentrations of glucose, but in higher glucose concentrations this decrease was said to be much less marked. The oxygen consumption in darkness could be described by the equation for a monomolecular process, but this was not true of the oxygen uptake in light. If the dependency of the light effect upon temperature and substrate concentration is of general validity, it may perhaps account for many of the discrepancies noted by other workers.

The effects of various spectral regions, obtained by means of filters, on the formation of gas by *Bacillus proteus vulgaris* were singularly consistent for a wide variety of substrates (117). In comparison with the dark control, the relative average gas production was 1.6 in green, 1.2 in yellow, 1.1 in white, 0.9 in red, and 0.6 in blue light. The intensities of the different wave-length bands do not appear to have been equalized.

In 1882, Wilson, in a brief paper, mentioned that light was without appreciable influence upon the carbon dioxide evolution of unspecified mushrooms. Although experimental details were omitted, it was stated that the temperature was controlled. Shortly thereafter, Bonnier and Mangin published the results of a large number of experiments which appear to have been carefully done and fairly well controlled, although the air temperatures were read presumably only to 0.5° (25). Carbon dioxide evolution, oxygen consumption, or both simultaneously, were measured, using both continuous aeration and constant volume methods. Diffuse sunlight was used as the source of illumination, and athough no intensity measurements were made, the effects of high and low intensities were compared in a few cases. In all, there were 18 experiments with the fruiting bodies of *Polyporus versicolor, Agaricus velutipes, A. conchatus, A. campestris* and *Telephora tremelloides,* and with mycelium of *Phycomyces nitens.* Without exception higher rates of respiration were observed in darkness than in light, the difference varying from 2%

to 56% and averaging about 23%. Reduction in respiration was somewhat greater with the illumination of higher intensity. On the average, the light effect was the same whether measured as carbon dioxide evolution or as oxygen consumption, and the respiratory quotient remained substantially the same in light and in dark. In general, the respiration was measured during successive light and dark periods of one to three hours duration. There is no evidence in the data which would indicate that the influence of the illumination conditions carried over into the subsequent dark period.

Bonnier and Mangin compared also the effects of the shorter and the longer portions of the visible spectrum from sunlight; the separation was effected by means of either filters or a prism. No attempt was made to equalize the incident intensities, but if an approximately equal energy separation can be assumed for the prism experiments, it was found that the reduction in respiration occasioned by illumination was due almost entirely to the yellow-red region, the blue-green portion of the spectrum having relatively little influence. The filter experiments, although of less value for the reason mentioned, pointed to the same conclusion.

Purjewicz noted that only in the very young stages and in the mature condition does the respiration rate of mushrooms remain constant over a period of several hours, even under constant environmental conditions, and he suggested that disregard for this situation may have introduced an error in the results of Bonnier and Mangin. The consistency of the data of these workers, however, seems to discount the possibility that such an error could have been of a magnitude sufficient to alter the trend of the results. Purjewicz measured the carbon dioxide production in a series of successive light and dark intervals of 30 to 90 minutes each. Illumination was provided by diffuse sunlight, filtered through a layer of water. The temperature of the respiration vessel was held constant within a few tenths of a degree. Forty-three experiments were performed with the following species: *Agaricus campestris, A. integer, A. melleus, Amanita phalloides, Armillaria mellea, Boletus edulis, Cantharellus cibarius, Lactarius deliciosus, Polyporus versicolor.* With a single exception all the experiments confirmed the findings of Bonnier and Mangin that the respiration rate was lower in light. Omitting the one aberrant case, the ratio light rate/dark rate varied between 0.58 and 0.90, and the average decrease of the respiration rate in light was

22%. The data give no suggestion of an after-effect of one period on the following.

Twelve additional experiments were made by Purjewicz comparing the relative effectiveness of red and blue light obtained by means of filters. It was observed that the reduction of respiration in the red light was approximately equal to that in white light, whereas in blue light the effect was only about one-fourth as great. The quantitative significance of these values is somewhat doubtful, however, in view of the lack of information as to relative intensities of the two spectral regions used.

In the same year Elfving reported the results of an investigation on the carbon dioxide production of several species of molds (*Briaraea* sp., *Aspergillus niger, A. flavescens, Mucor racemosus, Penicillium glaucum*) measured during successive dark and light intervals of one to two hours each. Illumination was provided by direct or diffuse sunlight filtered through water and glass. The temperature was controlled within 0.7°. In 25 experiments with 4- to 19-day-old cultures growing on a variety of organic substrates, there was found no effect of light greater than the experimental error of measurement which was stated to be about 12%.

In further experiments with *Briaraea* and *Penicillium glaucum* designed to test the possibility that a different behavior might be found in younger cultures, Elfving measured the total carbon dioxide liberated during the first few days following inoculation, in duplicate cultures growing in daylight or in darkness. In most cases the carbon dioxide production was considerably greater in the dark, the ratio carbon dioxide produced in light/carbon dioxide produced in dark ranging from 0.37 to 1.0. The smallest differences were found in the media containing peptone. The author concluded that these results were in complete agreement with those of Bonnier and Mangin (25). However, the results of these experiments are complicated by differences in growth, inasmuch as the dry weights of mycelium produced were also greater in darkness than in light. On the basis of carbon dioxide evolved per unit dry weight of mycelium produced, the differences between the illuminated and non-illuminated cultures were relatively small; the average ratio carbon dioxide produced per unit dry weight in light/carbon dioxide produced per unit dry weight in dark for all the experiments equalled 1.10. Considering the variability of replicate experiments, this does not appear

to indicate a significant difference between light and dark cultures. The average value of the above ratio for the various culture media without peptone was 1.19, whereas for those containing peptone it was 0.98. The significance of this difference is not clear, but it suggests that the composition of the substrate may play, directly or indirectly, an important rôle in the respiratory response to light.

A few additional experiments with young cultures, similar to the above, were carried out to compare the respiration in blue and in yellow-red light. The total carbon dioxide evolved was greater in the blue light, but on the basis of carbon dioxide produced per unit dry weight, there was no significant difference.

Detmer (1880, p. 271; 1882, vol. 2, p. 133; 1893) repeatedly referred to his experiments on respiration of fungi, reporting without any details his finding that the respiration is the same in light and in darkness. Aereboe reported a few experiments with young fructifications of *Agaricus campestris*. He could observe no effect of direct sunlight (filtered through 30 centimeters of alum solution) on rate of carbon dioxide evolution.

Using a technic essentially similar to that of Purjewicz, Shorawsky studied the influence of light on respiration of *Agaricus campestris, Phycomyces nitens* and *Mucor* sp. The alternate light and dark periods were of 20 to 60 minutes duration. No details as to the age or culture conditions of the material were given. The results with *Agaricus* confirmed those of Bonnier and Mangin (25) and of Purjewicz; in 10 experiments the average ratio carbon dioxide produced in light/carbon dioxide produced in dark was 0.82. A stimulatory effect of light on respiration was observed with *Mucor;* the average ratio for 12 experiments was 1.17. With *Phycomyces* the individual experiments were rather inconsistent: of six experiments two gave an increase, two a decrease, while two showed no significant difference; the average value of the ratio carbon dioxide in light/carbon dioxide in dark was 1.02. Aside from the somewhat erratic results with *Phycomyces* the data contain no suggestion of a carry-over of the effect from one period to the next.

Kolkwitz measured carbon dioxide production by *Aspergillus niger, Penicillium* sp., *Mucor* sp., *Oidium lactis, Micrococcus prodigiosus* and *Proteus vulgaris*. An electric arc with a metal reflector provided radiation intensities up to 60,000 meter-candles. It

was stated that the infra-red was filtered out in all cases and the ultra-violet also in some. Temperature was apparently carefully controlled. In most of the experiments the nutrient medium in which the culture had grown was replaced a day or two before the respiration measurement by water, by sugar solution, or by fresh nutrient medium. Since, under some conditions, oxalic acid is decomposed by light with liberation of carbon dioxide, the author discarded all experiments in which oxalic acid was present at the end of the run. Usually the respiration rates were sufficiently great so that several measurements could be made during each light and dark period. Despite a considerable variability of the respiration rate which was frequently found under constant conditions, most of the experiments with *Aspergillus* and *Penicillium* showed an unmistakable increase of respiration in light. This increase, which amounted to 5% to 20%, was usually transient, the respiration curves passing through a maximum at about 15 to 30 minutes after the start of illumination. The results with the other organisms, while not as clear cut, also indicated a greater respiration in light than in dark. Kolkwitz stated that the light effect was the same whether high or low intensities were used. An experiment with *Aspergillus,* in which the blue end of the spectrum was filtered out, also gave a stimulation.

More or less similar experiments were performed by Maximov, who attempted to reduce the irregularities in the dark respiration rate by more adequate provision of nutrient. Using *Aspergillus niger,* he found that the influence of light was related to the age of the culture and to the nutrient conditions. With an abundant nutrient supply the respiration of young cultures was not affected by illumination (of unspecified intensity) furnished by an electric arc lamp; exposure to direct sunlight, however, did result in an increased rate. Even with the artificial source a clear-cut stimulation was observed with young cultures deprived of nutrients and in old cultures regardless of the nutrient supply. The increase in respiration rate, which amounted to 10% to 40%, was manifested in the first measurement after illumination (usually 30 minutes) and thereafter became progressively smaller. With a long series of alternate light and dark periods repeated stimulations could be observed. Light was found to increase the respiration also of *Mucor stolonifer* during the first 30 minutes, but subsequently the mold appeared to be injured.

An improvement in technique was introduced by Löwschin who measured the temperature of the respiring material itself, as well as that of the thermostat. The species studied were *Aspergillus niger, Cladosporium herbarum, Oidium lactis* and *Penicillium* sp. Illumination was furnished by diffuse daylight filtered through water and glass. In all, 22 experiments were performed from which the writer concluded that no regular increase of respiration unconnected with heating of the culture was ever found. Examination of the data presented reveals, however, that the results were rather inconsistent. Thus, in one experiment during a 30-minute light period, the respiration rate increased 10% while the temperature rose 0.5°; in the 30-minute dark period immediately following, the respiration increased by an additional 5%, although the temperature decreased 0.2°. Löwschin did not determine the temperature coefficient for the dark respiration of the material used, so that one can not be certain that the temperature increases noted could indeed explain the observed respiration increases. Furthermore, in at least two experiments illumination was accompanied by a decrease in respiration.

Richards (250) measured carbon dioxide production, and in some cases also oxygen absorption, by young sporophores of *Marasmius conigenus, Polyporus adustus, Coprinus comatus, C. micaceus, Hypholoma fasciculare, Lactarius quietus* and *Polystictus versicolor*. Experimental data were not given, but it was stated that no significant difference in respiration rate was found in dark and in weak diffuse daylight or electric light of moderate intensity. On the average, the respiratory quotients were also identical in light and in dark.

De Boer, working with mycelia of *Phycomyces blakesleeanus* and *Polyporus destructor* and small fructifications of *Lactarius rufus* and *Laccaria amethysta,* was unable to detect any effect on respiration by diffuse daylight or electric light at intensities of 800 or 6,000 meter-candles. According to Pasinetti and Grancini, 25- to 50-minute exposure of *Alternaria brassicae* to direct sunlight resulted in a diminution of the subsequent rate of gaseous exchange.

In disks of young fructifications of *Psalliota campestris,* Föckler observed a 27% increase of oxygen uptake during the first hour of exposure to sunlight; in the next hour of illumination the respiration remained nearly at this higher level and then on subsequent darkening fell to the original dark value. There was little or no after-

effect of the light treatment. A similar rise in respiration was produced also by incandescent lamp radiation from which the infra-red and long visible red had been filtered out. Others stated that the rate of oxygen consumption by molds and bacteria was not influenced by exposure to red or blue light (of unspecified intensity) (197).

Considering the work on fungi as a whole, the discordant findings of the various investigators are very striking. Of the experiments using mushroom sporophores, the most extended and consistent data are in rather good agreement, showing a decrease of about 20% in light (25, 241, 272). Of the investigators who reported no effect of light on respiration, some do not present the experimental data (68, 69a, 69b, 250, 323), while others performed only a limited number of experiments (3, 64). The sole claim of an increased respiration in light was apparently on the basis of only two experiments (88).

The results with molds are even less consistent and give evidence that the condition of the material, as well as the nature of the substrate, may profoundly modify the influence exercised by light. None of the investigators seems to have attempted to control the illumination conditions prior to the respiration measurements, a factor which, conceivably, may play an important rôle, especially in view of the marked influence of light on development. The factor of culture age which appears to be of considerable significance may possibly be related to the development and maturation of spores which would tend to affect the light-absorbing properties of the culture. It should be mentioned, however, that the presence or absence of spores seemed to make little difference in the light stimulation in some of Maximov's experiments, while de Boer found that in cultures of *Phycomyces* on bread the sporangiophores were responsible for only 10% to 15% of the total respiration.

Of the indirect explanations which have sometimes been advanced to account for the observed light effects, temperature increases on illumination could scarcely explain the cases of decreased respiration. Furthermore, Kolkwitz obtained similar stimulations at 27.5° and 41°, temperatures at which the temperature coefficients might be expected to differ greatly. A purely photochemical decomposition of organic acids, such as is well known to occur *in vitro* (*e.g.*, 71, 78, 235), could perhaps explain some of the stimulations ob-

served; again, this would not be true of those experiments which showed a decreased respiration in light. None of the work with molds has included measurement of the respiratory quotient. Such measurement would appear to offer a possible means of detecting photoxidations of organic acids, since the ratio of carbon dioxide produced/oxygen consumed is greater than unity for such reactions.

While the experimental methods have scarcely been adequate to yield an unequivocal result, it may be stated that there is no clear-cut evidence in any of the work of an after-effect of a light treatment on the subsequent dark respiration. In the experiments in which the rôle of light quality has been studied, the long wavelength end of the spectrum has usually been claimed to be the effective portion, whether in inducing a stimulation (154) or an inhibition (25, 241) of the respiration.

The majority of workers who have studied the influence of visible radiation on yeasts have found the respiration rate unaffected; the sole exception is van der Paauw. Stimulation of the fermentation rate, on the other hand, has been reported by several, though not all, investigators. From the three studies dealing with bacteria it has been concluded, respectively, that the respiration is stimulated, inhibited and not influenced by light.

This cataloging of the results of previous investigators is not intended to carry the implication that such a procedure is capable of demonstrating the truth or falsity of any given report. The conclusion to be drawn from the complete lack of agreement would appear to be that each particular type of material must be subjected to much more intensive study with proper regard for the many factors which may influence its reactions. Indeed, because of the variety of experimental subjects, conditions and technics which have been employed in the several investigations, comparisons among them may not be justified at all.

Normally chlorophyll-deficient organs and tissues of higher plants. *a.* Flowers and Fruits. Cahours reported the results of experiments on the respiration of flowers but gave no experimental details (51). According to Aereboe, *Ranunculus* spp., Liliaceae, *Nymphaea alba, etc.,* were used. The carbon dioxide production was stated to be, in general, slightly greater in light than in dark, the difference being much more marked in pure oxygen than in air. Flowers of *Salvia*

pratensis freed of all green parts were found to produce 4% to 20% more carbon dioxide in diffuse light than in darkness, the temperature of the respiration vessel remaining constant (69). No such increase was observed with flowers of *Syringa vulgaris* or with petals of *Rosa,* which the author considered as additional evidence that the positive results with *Salvia* were not due to a heating effect.

Using methods similar to those described above in the section on fungi, Bonnier and Mangin (26) studied the respiration of inflorescences of *Arum maculatum, Hyacinthus orientalis* and *Robinia pseudo-acacia.* The *Arum* inflorescences were stated to be free of chlorophyll. In the experiments with hyacinth and locust the bases of the inflorescences were inserted in moist soil in the respiration chamber; after the respiration was determined the flowers were picked off and the measurements repeated with the peduncles alone, using air containing carbon dioxide. Bonnier and Mangin published only the results after correction for the photosynthetic activity of the green parts. Their data show a 14% to 34% reduction of respiration during the period of exposure to daylight. The respiratory quotient was the same in light and in dark. Small temperature changes would not appear to be of importance in this work, since in the experiment with *Robinia* a difference of 3° did not produce any alteration of the dark respiration rate.

The respiration rates of allegedly chlorophyll-free flowers of *Lilium candidum* and *Nymphaea alba,* as well as of chlorophyll-containing inflorescences of *Lathraea squamaria,* were measured by Purjewicz. Although the temperature was controlled within quite narrow limits, the results were so irregular that they seem of little evidential value.

Aereboe carried out an extensive series of experiments with petals of *Taraxacum officinale, Syringa vulgaris, Paeonia, Salvia pratensis, Crepis biennis, Chrysanthemum leucanthemum, Papaver rhoeas,* garden aster, *Rosa centifolia* and some other roses. All the material was shown by spectroscopic examination to be free of chlorophyll. The temperature was measured by a thermometer in the respiration vessel with its bulb surrounded by the respiring material. Interpretation of several of the experiments is rendered difficult by a continuous fall in the respiration rate with time. In those instances where this was not the case, the difference between respiration in

dark and in diffuse or direct sunlight fell within the range of experimental error. It has been pointed out by de Boer, however, that there may be some question as to whether the petals were not packed so closely in Aereboe's experiments that only a small fraction of the material was actually exposed to the light.

Chlorophyll was presumably present in most of the flowers studied by Curtel, so that the larger part of his data does not appear to be of significance for the problem here considered. In *Phlox paniculata,* of which it was stated that the green parts were restricted to the very small calyx, both the carbon dioxide production and the oxygen consumption were appreciably less in diffuse sunlight than in darkness. Montfort and Föckler stated, without further details, that the ratio of respiration in sunlight to that in darkness for the chlorophyll-poor inflorescences of *Neottia nidus avis* was 1.57.

Ranjan and Saksena measured the rate of carbon dioxide production of flowers of *Canna, Nerium* and *Bougainvillea* before, during and after an 8- to 12-hour period of exposure to the radiation, presumably filtered through water and glass, of a 1,500 watt lamp at about one foot distance. In *Canna* only a slight indication of a respiration increase was found. The carbon dioxide evolution of the *Nerium* flowers, on the other hand, rose after a few hours of exposure to about one and one-half times that of the initial dark rate and remained nearly at this level during the rest of the illumination period. In the subsequent dark period the respiratory stimulation persisted for many hours in the pink-colored flowers, whereas yellow flowers exhibited only a small and transient after-effect. The flowers of *Bougainvillea* showed an increase of about 40% during the first two hours of illumination, but on continued exposure the rate returned nearly to the previous dark value. From some rather crude estimates of the amounts of carotenoids and anthocyanins present in the various flowers, the authors concluded that the light effects were correlated with the pigment concentration.

Cahours, who measured the oxygen absorption and carbon dioxide excretion by ripe apple, orange and lemon fruits, stated that the proportion of carbon dioxide produced was considerably greater in diffuse light than in darkness (50).

b. Seeds and Young Seedlings.[2] As a matter of historical interest

[2] In this section are included references to young seedlings which might be expected to exhibit little or no photosynthetic activity, though germinated in light. Studies of older seedlings cultured in darkness, so as to prevent chlorophyll formation, are discussed below in the section on etiolated plants.

mention should be made of the experiments of Pauchon, although they do not appear very decisive for the problem under consideration. This worker measured the gaseous exchange of several species of seeds which were permitted to germinate in light or in darkness for a period of 4 to 11 days. In 10 of 12 experiments the oxygen consumption was 20% to 95% greater in the light. Carbon dioxide production was more nearly constant under the two conditions; as a result the respiratory quotient was always greater in darkness. In these experiments no attempt was made to control the temperature, and in some cases the degree of germination and development differed in the light and dark sets; these circumstances may perhaps suffice to explain the observed results.

Bonnier and Mangin (26) measured both carbon dioxide production and oxygen absorption by young seedlings of *Lepidium sativum, Linum usitatissimum, Lupinus luteus* and *Faba vulgaris* during alternating light and dark periods of one to two hours. In all of the 13 reported experiments the respiration was higher in darkness than in daylight by an amount up to 46%, the average difference being about 15%. The magnitude of the effect was said to vary directly with the light intensity. The authors stated that the retarding influence of light on respiration was smaller during the early stages of germination, a result which they regarded as being due, in part at least, to the opacity of the seed coats; it was found, indeed, that the light effect was less in seeds with opaque coats than in those with transparent integuments. The carbon dioxide/oxygen ratios found by Bonnier and Mangin were quite low, ranging from 0.30 to 0.87. Since the photosynthetic quotient may be assumed to be unity, the occurrence of an appreciable amount of photosynthesis would be expected to result in a lower carbon dioxide/oxygen ratio in light than in darkness. As there was no consistent indication of such a difference, it may be concluded that, notwithstanding the presence of chlorophyll in some of the seedlings used, photosynthetic activity was not sufficiently great to account for the observed light effects.

Respiration of barley and wheat germinating in diffuse daylight and in darkness was measured by Day, presumably with a high degree of accuracy. Although the light-grown seedlings were apparently capable of some photosynthesis, the author concluded, from experiments in which the respired carbon dioxide was not allowed

to accumulate, that light had a small stimulatory effect on the respiration, amounting to about 4% or 5%, whether measured in terms of carbon dioxide or of oxygen.

Becquerel measured the gaseous exchange which had occurred during a five-month period of storage in light or in darkness of various dormant seeds, seed coats and seeds with the integuments removed. Since the respiratory quotients, in general, departed quite widely from unity, there must have occurred a change in volume or pressure during the experiment. It is not clear from the published data that correction was made for this change. Interpretation of the data is handicapped also by a number of misprints or other errors. Despite these uncertainties the general result is very clear: in every case the illuminated material had respired to a greater extent than the dark material. The difference varied from 20% to 570%. The same general result was found in both carbon dioxide production and oxygen consumption, although quantitatively the effect was in some cases quite different by the two methods; in other words, the respiratory quotients differed in light and in dark. The significance to be attached to Becquerel's findings is rather doubtful in view of *a*) the lack of any mention of temperature control, *b*) the total absence of respiration in four of the dark experiments, and *c*) the curious finding that in castor beans, peas and beans the respiration of the integuments alone was as great as or greater than that of the intact seeds or of the seeds minus the coats.

In respiration studies of seeds of *Cucurbita pepo,* with seed coats removed, irradiation by moderately high intensity electric light, with the infra-red filtered out, produced a 20% increase during the first hour (88). In sunlight a 56% increase was noted; during the second hour of illumination the rate was only about 35% higher than in the initial dark period, and on subsequent darkening it fell to the original dark value. Sunlight from which the ultra-violet was removed by ordinary glass caused only about one-half the effect found when a Uviol filter, transmitting the longer ultra-violet, was used.

Quite different results were found with isolated cotyledons of *Cucurbita pepo* (45). One cotyledon was exposed continuously to light of about 100 foot candles intensity; the other cotyledon from the same seed was kept in darkness. Measurements of the gas ex-

change were made at intervals from the 18th to the 48th hour after excision. In the darkened organ the respiratory quotient remained at about 0.6 throughout this period. In light the initial rate of oxygen consumption was only one-third that in darkness, while the rate of carbon dioxide production was about one-half; the respiratory quotient was 0.9. Thereafter the rate of gaseous exchange of the illuminated cotyledon approached that in darkness and the respiratory quotient gradually fell to 0.7. Brown suggested that light retarded the conversion of fat to carbohydrate.

A rather special case is furnished by seeds whose germination is influenced by light, the so-called light-sensitive seeds. With tobacco seeds which require a light exposure to initiate germination, a relatively short irradiation period resulted in an immediate and persistent increase in respiration rate (measured either as carbon dioxide evolution or as oxygen absorption) over that of the unilluminated controls (152, 265). Schröppel found, further, that appreciable increases in the catalase and peroxidase activities of the seeds did not occur until several hours after the light treatment.

c. Roots. In a single experiment on the oxygen consumption of excised roots of *Vicia faba* during alternate light and dark periods, no significant differences were observed (310). Chlorophyll-free roots of *Phaseolus multiflorus, Primula officinalis, Sedum maximum, Vicia faba* and *Zea mays* were also investigated (241). The successive respiration determinations showed marked irregularities. These were in turn reflected in the results which often were inconsistent even for a single species. Aereboe performed three experiments with excised *Vicia faba* roots. The differences found appear to be within the limits of experimental error.

Montfort and Föckler, and Föckler described experiments concerning the influence of light on oxygen uptake of excised roots of *Hyacinthus candicans* and *Vicia faba.* Illumination by electric light minus the infra-red, or by sunlight, gave increases of 15% to 100% over the dark rate. At the higher intensities used, the maximum increase occurred during the first hour of irradiation; on continued exposure the respiration fell to a more or less constant value below this maximum but still above the dark level. On subsequent darkening the respiration returned nearly or quite to the original dark value, and a second stimulation similar to the first could be evoked by further illumination. In the *Vicia faba* experi-

ment, which was stated to have been done in sunlight of lower intensity, the first increase on illumination was maintained during a three-hour exposure period.

The effect of intensity was studied with the incandescent lamp source. The stimulation was roughly proportional to intensity over the range covered (stated to be approximately from 4.5% to 20% of the intensity of the summer noonday sun).

The rôle of light quality was studied by means of various filter combinations which furnished equal energy values in the regions: 600 to ca. 700 mμ, 470 to 620 mμ and ca. 400 to 500 mμ. The stimulations found were: red, 7%; green, 10%; blue, 37%. The spectral effectiveness curve agrees fairly well with the absorption curve for the etiolated leaf, as determined by Seybold. The infra-red region appears to be without effect, since nearly identical results were obtained with electric light whether the infra-red were filtered out or not. The influence of the ultra-violet was examined by comparing sunlight transmitted through ordinary glass and through Uviol glass; white light alone caused a 22% stimulation, whereas the white light plus ultra-violet produced a 33% increase.

It was also found by Föckler that roots which had been growing exposed to light for some days prior to the respiration measurements showed a much smaller initial stimulation on illumination, from which he concluded that the roots can become light-adapted.

Mothes, Baatz and Sagromsky stated, without details, that the rate of oxygen consumption of roots was not influenced by exposure to red or blue light.

Using the Fenn microrespirometer, with excellent temperature control, Marsh and Goddard made some incidental measurements of the oxygen uptake by carrot root slices in darkness and in light. The radiation was provided by a 100-watt Mazda lamp at 10 centimeters distance. The results of only a single experiment are shown in detail, the readings being taken at 20-minute intervals. During an hour's illumination the respiration rate was fairly constant but only about 75% as great as that in the preceding dark period. A further reduction to approximately 60% of the initial dark value was found during an hour of darkness following the exposure. In the three additional experiments for which the results are reported, the ratios of light respiration/dark respiration were 0.88, 1.02, and 1.40.

d. Tubers. The oxygen consumption of disks of potato tubers was found to increase by 21% during the first hour of illumination by incandescent electric light, minus the infra-red, at an intensity approximately one-fifth of noon sunlight; exposure to full sunlight resulted in a 51% rise over the dark rate. During the second hour of illumination the respiration fell nearly to the dark value (88).

e. Rhizomes. Bonnier and Mangin (26) determined gaseous exchange by rhizomes and adventitious roots of *Solidago virgaaurea* and *Epilobium spicatum* in darkness and in sunlight. In light the carbon dioxide production was 10% to 34% less than in darkness, while the oxygen consumption was decreased by only 4% to 16%. As a consequence, the respiratory quotient was, in all cases, somewhat smaller in light. No significant effect of light on the carbon dioxide evolution by rhizomes of *Polygonatum multiflorum* could be observed by Purjewicz in a limited number of experiments.

f. Buds. Bonnier and Mangin (26) found no difference in the carbon dioxide production by unopened buds of *Aesculus hippocastanum* in light and in dark. The authors suggested that the lack of effect may have been due to the opacity of the bud scales. Johansson's (141) measurements of carbon dioxide production by young fronds of *Polypodium vulgare,* prior to development of the photosynthetic capacity, indicated that light does not influence the respiration.

Surveying the work on flowers, seeds, roots, tubers, rhizomes and buds as a whole, it seems fair to say that, while very few of the investigations are free from methodological objections of one kind or another, there are definite indications that radiation influences the rate of respiration in some materials. For the most part increased gas exchange has been observed as the result of irradiation, although in a few instances the opposite effect has been found. The experiments thus far reported are to be regarded as exploratory in nature. In no case have there been carried out systematic studies employing adequate experimental technics with sufficient attention to the biological factors involved.

Saprophytic, parasitic, albinic and variegated angiosperms. Drude measured the carbon dioxide production of entire flowering plants of *Monotropa hypopitys* at one- to five-hour intervals over a three-day period, during which they were exposed to diffuse sunlight during

the day. From several experiments, for which the data were not published, the author concluded that the illumination had no consistent influence on the respiration rate, although in a number of cases the carbon dioxide evolution was greater during the day. It does not seem possible to determine, from the recorded data, the extent of the temperature fluctuation of the respiring material.

Wilson, in a preliminary account which apparently was never followed by a more extensive publication, stated only that in numerous experiments with *Orobanche, Monotropa* and *Hypopitys* there was no effect of light on carbon dioxide production.

In the experiments of Bonnier and Mangin (26), plants of *Monotropa hypopitys, Orobanche epithymum* and *Neottia nidus-avis,* together with considerable amounts of soil and humus, were used. As the substrate was not illuminated its gaseous exchange was assumed to remain constant. In light the respiration was decreased by 13% to 44%; quite similar results were found for both the carbon dioxide production and the oxygen consumption.

Groner compared the carbon dioxide production by albino corn seedlings in darkness and when exposed to Mazda illumination of moderately high intensity filtered through water. No differences outside the experimental variability (which was probably of the order of several per cent) were found when the plants were illuminated continuously or kept in darkness during a three-and-one-half-day period. In two experiments, in which the irradiation followed a period of darkness, respiratory increases of approximately 50% and 100% were observed.

In one of these the maximal stimulation occurred during the first two-hour period of illumination; by the end of 21 hours in light (and possibly much earlier) the rate had returned to the initial dark value. The other experiment showed a slight diminution of respiration during the first two hours of exposure, the maximal increase occurring in the succeeding two-hour interval; in this case, too, the stimulation was only transient. There seems to be a suggestion in the published curves that a slight increase in respiration occurred also when the plants were darkened after a light exposure.

Van der Paauw found an increase of the order of 35% in the oxygen consumption by detached leaves of *Oplismenus* during irradiation. The radiation was presumably furnished by a 150-

watt lamp at about 13 centimeters distance, filtered through eight to nine centimeters of water and applied for an hour. Following exposure the respiration returned to the original dark value. Ranjan (242, 244, I) reported the results of experiments with detached chlorophyll-poor leaves of *Croton*. During exposure to the radiation, filtered through water and glass, of a 1,000-watt lamp at about one foot distance, the rate of carbon dioxide evolution was approximately 25% greater than that in the preceding and subsequent dark periods.

Parija and Saran measured the carbon dioxide production by detached albinic and variegated leaves of *Aralia* before and after illumination. The radiation was produced by a 60-watt Argenta lamp at 10 inches distance and was filtered through a layer of water. Various spectral regions were isolated by means of Wratten filters. Although it is stated that the intensity was the same in all cases, it is not clear that this refers to the light incident on the leaf. Illumination was without influence upon the respiration rate unless the detached leaves had been kept previously in darkness for two to three days. In such starved leaves respiratory increases, presumably as great as 150%, were elicited by irradiation. Exposure for seven and one-half minutes was as effective as that for two hours. The greatest increase was produced by violet light; blue and white light were considerably less effective, while red light was inactive. Parija and Saran found also that the reducing sugar content of the starved leaves was greatly increased by a seven-and-one-half-minute exposure. Based upon the sugar content of the leaf prior to illumination, the increase varied from 100% to 700% in several experiments; the absolute gains per unit weight of leaf were quite uniform, however.

The conclusions expressed at the end of the preceding section would appear to apply equally well to the experiments with albino plants, saprophytes and parasites.

Etiolated plants. The earliest measurements of the influence of light on respiration which have come to the reviewer's attention are those of Morot (1849), made incidental to a study of chlorophyll formation. Excised etiolated oat leaves were found to produce 0.84 cc. of carbon dioxide in darkness, and 1.2 cc. in direct sunlight, in which case they remained yellow; in diffuse sunlight 0.82 cc. of carbon dioxide was evolved, the leaves becoming green. The temperature was not controlled or measured.

Von Wolkoff and Mayer reported results typical of a large number of experiments on oxygen consumption by etiolated seedlings of wheat, nasturtium and buckwheat; in some experiments the cotyledons and/or leaves were removed. The temperature fluctuated rather widely and the analytical error was relatively large with respect to the magnitude of the respiration rates. Exposure to sunlight, or to sunlight with the red region filtered out, resulted in some cases in small but consistent increases in respiration, whereas in others no marked differences were found. The authors expressed uncertainty as to whether the observed effects were to be ascribed to a real stimulation which occurred only under certain conditions or to limitations of the technic employed. Wilson observed no effect of light on the respiration of etiolated seedlings of various species.

In a limited number of experiments with etiolated seedlings of *Ricinus communis, Lepidium sativum, Triticum sativum* and *Linum usitatissimum,* Bonnier and Mangin (26) consistently obtained a smaller respiration in light. The decrease amounted to 11% to 26% when measured as carbon dioxide evolution; in two experiments in which oxygen absorption was determined simultaneously the decrease was only 4% and 6%. Purjewicz measured carbon dioxide production by etiolated seedlings of *Zea mays* and *Lepidium sativum* at low temperatures (4° to 6°) in order to prevent chlorophyll formation during the illumination. Although the data for the five individual experiments are somewhat irregular, all showed, on the average, a greater respiration in light by 4% to 22%.

Yellow chlorophyll-poor cells of *Chlorella* incapable of photosynthesis were obtained by culturing in a sugar-containing medium low in iron (79). From measurements of the gas exchange, it was concluded that the respiration of such cells is the same in light as in darkness. There may be some question as to the validity of this conclusion, however, since the method employed depends upon a knowledge of the value of the respiratory quotient, which was not determined. It has been shown by others that the R.Q. of many green algae in the presence of sugar is not unity, and it may possibly differ in light and in darkness.

Föckler observed a 31% increase in absorption of oxygen during the first hour of exposure to sunlight of disks of young etiolated shoots of *Asparagus officinalis.* During the second, third and fourth

hours of illumination the increases over the dark rate were approximately 20%, 19% and 12%, respectively. In the following dark period the rate returned to the original dark value. Illumination by electric light minus the infra-red, at about one-fifth full sunlight intensity, resulted in only a 7% rise in respiration.

The influence of white light on carbon dioxide production by etiolated barley seedlings has been studied, using the spectrographic method of analysis (143, 316a). On exposure to light of fairly low intensity (180 foot-candles or less), no significant alteration of the rate of carbon dioxide excretion was apparent during the first half hour. Following this, the plants, whether continued in light or darkened, exhibited a rate of respiration which increased to a maximum only after some hours, and then gradually decreased. By 24 hours after a half-hour period of illumination, the dark respiration was substantially the same as that before exposure. At this time a second exposure to light again resulted in an increased rate of carbon dioxide production similar to that previously observed.

The magnitude of the respiratory stimulation was dependent upon the intensity and duration of the irradiation. At an intensity of 60 foot-candles, exposures of 5 or 10 minutes elicited only insignificant effects, whereas illumination for 20 minutes or longer resulted in marked increases. With an exposure time of 30 minutes, the magnitude of the increase in respiration rate, which was relatively independent of the intensity in the range 50 to 500 foot-candles, was approximately 20%. Smaller stimulations were evoked by either higher or lower intensities.

For the most part, the data so far available are insufficient to permit definite conclusions as to the influence of radiation upon etiolated plants. The results of Weintraub and Johnston, although of a preliminary nature, indicate that light induces an appreciable augmentation of the rate of carbon dioxide production by the etiolated barley seedling.

Chlorophyllous Plants

There exists a considerable body of data on the gaseous exchange of chlorophyllous plants which bears more or less directly on the problem of the influence of radiation on respiration. The work containing direct measurements of respiration under conditions in which photosynthesis appears to have been nearly or quite suppressed by the experimental treatment will be considered first, and

in a subsequent section there will be indicated some lines of evidence obtained with plants capable of assimilation. This division is to a certain extent merely an expression of interpretation, since it is sometimes impossible to determine whether or not photosynthesis is entirely absent.

Direct evidence under conditions in which photosynthesis is suppressed. It should be emphasized that since there is no certainty, in any of the experiments reviewed in this section, that photosynthesis is entirely absent, only those results which show a greater apparent respiration in light than in darkness can be regarded as significant. Furthermore, the possibility should not be ignored that the methods employed to inhibit photosynthesis may themselves exert an influence on the respiration response to irradiation.

In many investigations of the diurnal course of assimilation under "natural" conditions, there have been demonstrated minima in the apparent rate of photosynthesis during the period of highest light intensity (and of highest temperature). In some instances actual excretion of carbon dioxide at a rate greater than that of the normal dark respiration has been observed (*e.g.,* 157–159, 300). Marked fluctuations have been found also in the diurnal course of the respiration of plants kept in darkness (*e.g.,* 160). Since in such experiments many environmental factors are not controlled, the significance of these results is by no means clear.

a. Suppression of Photosynthesis by Chemical Agents. Bernard appears to have been the first to demonstrate a differential inhibition of photosynthesis and of respiration by chemical agents. This author found that treatment of *Potamogeton* and *Spirogyra* with chloroform caused cessation of oxygen evolution in light while carbon dioxide evolution continued. The photosynthetic capacity was restored on removal of the chloroform. No quantitative comparison of the rates of respiration of the treated plants in light and in dark was made, however. During the ensuing quarter century a number of investigators (for references see, *e.g.,* 150) studied the influence of various narcotics on the gaseous exchange of plants. This literature need not be reviewed here, since the methods employed were not adequate to yield quantitative information concerning the effect of light on respiration.

Measurements of carbon dioxide production by excised shoots of young barley plants and of detached *Prunus laurocerasus* leaves in

air containing chloroform vapor were made by Irving. A transient stimulation of respiration due to the chloroform itself was observed, but the rate was practically the same in light as in dark. Warburg (313, I) found that the addition of a small amount of *n*-dodecyl alcohol to an illuminated suspension of *Chlorella* in an alkaline carbonate-bicarbonate buffer irreversibly abolished the photosynthetic capacity and resulted in a greater oxygen consumption than in darkness. Complete inhibition of photosynthesis by a number of other substances was also reported (313, II), but in these instances the rate of oxygen consumption was stated to have been the same in light as in darkness.

Fromageot observed that the photosynthesis of *Ulva lactuca* was first very markedly retarded and finally completely suppressed in the presence of increasing concentrations of glycerine. The dark respiration was also decreased but to a much smaller extent. Although the temperature and illumination conditions do not appear to have been very well controlled, there seems to be no doubt that at glycerine concentrations above about 40% a much higher rate of oxygen consumption occurred in light than in darkness.

Shibata and Yakushiji, in a preliminary note, reported that small amounts of hydroxylamine hydrochloride completely inhibited photosynthesis in *Chlorella ellipsoidea* and *Ulva conglobata* without influencing respiration. The curve shown for *Chlorella* indicates that in the hydroxylamine-treated culture the oxygen uptake is identical in light and in darkness. The results seem much less clear-cut, however, in the more extensive data presented by Yakushiji. Thus, in *Ulva* the conclusiveness of the demonstration that hydroxylamine is without influence on respiration is somewhat vitiated by the inconstant respiration rate, even in the untreated control. Assuming that such is the case, however, the *Chlorella* data indicate a considerably higher respiration rate in light than in darkness, whereas in *Ulva* the reverse is the case. The measurements were made with the Barcroft differential manometer, but only one experiment with each species is mentioned. Although the results do not seem very decisive, the work suggests that hydroxylamine may prove to be a very useful substance for experiments of this kind and worthy of further investigation.

In a quite similar experiment with shoots of *Fontinalis antipyretica,* the rate of oxygen absorption in the presence of 0.001 M

hydroxylamine hydrochloride was decreased by only about 2% in darkness, whereas a reduction of approximately 13% was noted in light (302). As has been pointed out above, these findings of decreased apparent respiration in light may indicate merely an incomplete inhibition of photosynthesis.

Föckler measured the oxygen uptake by detached leaves of *Potamogeton lucens* in a 0.06% phenylurethane solution. The respiration rate of the leaves exposed to full summer noon sunlight rose by the end of four hours to more than twice that of the unilluminated leaves; on further exposure the rate diminished somewhat and, on darkening, it returned approximately to the level of the dark control. In comparable experiments with red (600 to 700 mμ), green (470 to 620 mμ), blue (400 to 500 mμ) and white light at about one-fifth of full solar intensity, the oxygen consumption was less than that of the dark control, the differences being most pronounced in the red and green light. Föckler attempted to explain these results by assuming that photosynthesis was not completely inhibited by the phenylurethane and hence tended to mask the respiratory stimulation. On this basis it was concluded that such a stimulation was produced by the white and blue radiation but not by the green or red.

Myers and Burr determined the oxygen consumption by *Chlorella vulgaris* in the presence of 0.01 M KCN over a wide range of measured light intensities. Between 1,500 and 22,000 foot-candles the net oxygen uptake increased with the intensity. Interpretation of experiments in which cyanide is used as a differential inhibitor of photosynthesis is somewhat complicated, both by the relatively large stimulation of the dark respiration induced by the substance itself and by the fact that, under certain conditions at least, the photosynthesis is only partially suppressed. For these reasons it is difficult to determine the lower limit of light intensity which influences the respiration, but it is clear that at intensities above about 13,000 foot-candles the respiration rate exceeded that in the dark; at 22,000 foot-candles the increase amounted to at least 40%.

b. Suppression of Photosynthesis by High Temperature. It has been observed that *Elodea canadensis* placed in water at 45° to 50° completely lost its photosynthetic capacity without any change in its ability to absorb oxygen (266). The authors stated, without furnishing any experimental data, that in such plants oxygen absorp-

tion and carbon dioxide liberation continued at the same rate in light as in darkness.

Kreusler measured the carbon dioxide exchange, at various temperatures, of detached leaves and shoots of *Ricinus* and *Prunus laurocerasus*. At 50° C., a temperature which produced signs of injury in the leaves, the carbon dioxide evolution during a two-hour interval, comprising one hour of electric arc illumination and one hour of darkness, was about one and one-half to two times as great as the rate in the subsequent dark period.

Jumelle studied the gaseous exchange, in daylight and in darkness, of several species of lichens, after exposure to elevated temperatures. Although the validity of the analytical method used has been questioned (185), and despite many irregularities in the data which appear to be due largely to individual variations among the plants, certain conclusions seem justified. Exposures of a few hours to several days at temperatures of 40° to 55° resulted in more or less complete suppression of photosynthesis; the extent of the inhibition depended upon the temperature and duration of treatment and upon the species. Following the less drastic treatments there was little or no depression, or even an augmentation, of the dark respiration. After longer exposures and higher temperatures the dark respiration was usually reduced, whereas the respiration in light was frequently increased, in some cases to several times that in darkness. In some experiments oxygen consumption and carbon dioxide evolution were affected to the same degree, but in others the respiratory changes were accompanied by marked alterations of the respiratory quotient.

Wurmser and Jacquot observed that after short exposures to elevated temperatures the photosynthesis (measured at approximately 16°) of *Ulva lactuca* was very markedly depressed, whereas inhibition of the dark respiration was much less pronounced. With two-minute treatments at temperatures above approximately 45° the rate of apparent respiration in light was two to three times as great as the dark respiration of similarly treated plants, although it did not attain the level of the respiration of the untreated dark controls.

Lichens apparently furnish especially suitable material for experiments of this type, since they are able to endure much higher temperatures than many other plants, while the photosynthetic mecha-

nism seems to be quite sensitive to elevated temperatures (see also 282, 283). It has been reported that marked reduction of photosynthetic capacity without change in dark respiration is exhibited also by *Chlorella,* following exposure to elevated temperature (151). A carefully controlled investigation of such organisms, employing modern analytical technics, would appear to offer considerable promise.

c. Suppression of Photosynthesis by Desiccation. Stocker observed that the rate of carbon dioxide production by thalli of *Lobaria pulmonaria,* collected in the air-dry condition, was only about 40% as great in darkness as when exposed to diffuse daylight of about one-fourth to one-third of full sunlight intensity. From Stocker's measurements of the temperature coefficient of the dark respiration, a temperature rise of approximately 8° would be required to account for the observed stimulation on the basis of a heating effect, which does not seem likely under the conditions of the experiment.

d. Suppression of Photosynthesis by Lack of Carbon Dioxide. Photosynthesis can be retarded by removal of the respired carbon dioxide as it is formed. However, since much of this carbon dioxide is produced at or quite near the chloroplasts, it is not possible, in practice, to remove all of it before a portion becomes available for assimilation. Hence the photosynthesis cannot be reduced to zero, and the apparent respiration, as measured by the oxygen consumption, will always be somewhat smaller than the true respiration. Any observed increase in respiration rate under such conditions represents, therefore, a minimal effect. Obviously, only increases in respiration can be detected with certainty by this method.

Measurements of the apparent respiration, in light and in dark, of several species of green plants in the absence of carbon dioxide have been made (26). Unfortunately, the published data are too incomplete to permit of any judgment of the results. In other experiments the rate of carbon dioxide removal appears to have been so slow that considerable assimilation was permitted (191).

Very clear-cut experiments have been made by using the manometric method with potassium hydroxide in the respiration vessel (303). Similar results were obtained with *Oocystis* sp. and with *Hormidium flaccidum.* During illumination (presumably by a 150-watt lamp at about 14 centimeters distance and filtered through 8 or 9 centimeters of water) the oxygen consumption was in some

cases more than twice that in the preceding dark period. On subsequent darkening the rate decreased, rapidly at first and then more slowly, returning to the initial dark level after about two hours. Repetition of the exposure at this time resulted in a second stimulation of the same magnitude as the first. An experiment in which the irradiation intensity was reduced to one-fourth gave approximately one-fourth the stimulation. Radiation longer than 600 mμ was apparently much less effective than the white light, although it is not entirely clear from van der Paauw's description whether the absorption by the water was considered in comparing the transmitted energies.

Using a quite similar technic, Bode measured the oxygen consumption of *Fontinalis antipyretica*. Following a 24-hour sojourn in darkness the respiration was measured successively in darkness; in blue light of about 10,000 lux for one-half hour; in red light, presumably of the same intensity, for one-half hour; and in darkness. The radiation was provided by a 2,000-watt lamp with a condensing lens and passed through colored solution filters. Two types of plant material were used, cultured for some weeks prior to the respiration measurements in either red or blue light, using filtered sunlight as the source. Very consistent results were obtained in a series of replicate experiments with each type. In all cases there was an increased rate of oxygen consumption during the periods following the initial dark measurement. The average increases for the blue material were 74% in blue light, 41% in red light, and 46% in the subsequent dark period. For the red material the corresponding stimulations were 64%, 46% and 50%, respectively.

As has been pointed out above, these increases are minimal effects, inasmuch as any photosynthesis which may occur through utilization of the respired carbon dioxide would tend to reduce the apparent respiration. In this connection it may be significant that in all cases the final dark respiration was actually slightly greater than that during the preceding period of red illumination, suggesting that some photosynthesis had occurred. It is interesting also that the red light exerted a somewhat greater stimulation on the plants cultured in red light, whereas the blue light produced the larger effect on the blue material.

Franck and French (91) have studied the influence of high light intensities on oxygen consumption of discs excised from leaves of

Hydrangea and other plants, using the manometric method in the presence of potassium hydroxide. The radiation employed was provided by tungsten filament lamps and filtered through water and glass. By means of a condensing system intensities up to 80,000 lux were obtained. In light of about one-half this intensity, the rate of oxygen uptake was approximately twice that of the preceding dark period; in darkness following the irradiation the rate remained, for a period of 10 to 30 minutes, several per cent higher than that before exposure. The rate in light was not constant, but decreased with time. The velocity of this decay in rate was said to depend upon the previous history of the leaf, on the light intensity and upon the oxygen concentration. Leaves which had been actively photosynthesizing or which had been immersed in sugar solution prior to the measurements were stated to show somewhat greater rates of oxygen consumption which remained constant for a longer time. One rather remarkable result was noted with such sugar-fed leaves: in darkness following a 25-minute light exposure the oxygen consumption was only about 20% greater than that during the initial dark period, whereas subsequent second and third exposures of identical duration and intensity were followed by increases of 87% and 98% above the initial value.

In 1.5% oxygen no light effect was observed. In 60% or 100% oxygen the stimulation of oxygen consumption was considerably greater than in air, whereas the rate of dark respiration was independent of the oxygen concentration over this range. From a comparison of results obtained with continuous light and with intermittent light of much higher intensity, the authors concluded that the light stimulation increases less than linearly with the intensity, at least at high intensities. In view of the inconstancy of the rates of oxygen absorption with time, however, it seems questionable whether such a conclusion is justified by the data presented from this indirect method.

Franck and French stated that experiments with filters of copper sulfate and of potassium dichromate showed large effects induced by red or blue wavelength bands, a result which is regarded as an indication that it is the chlorophyll which sensitizes the reaction. Spectral regions in which chlorophyll absorption is low do not appear to have been tested. The authors have calculated the order of magnitude of the quantum yield for the photoxidation which turns out to be about 0.01 in pure oxygen.

Leaf macerates and leaves killed by immersion in boiling water also showed increased oxygen uptake in light, which resembled closely that observed with living leaves. Because of this finding and that of the quite different relationships between oxygen concentration and oxygen uptake in light and in dark, it was concluded that the effect is a photoxidation unrelated to the normal vital respiration.

Mention should be made also of the work of Godlewski (1879) who compared the amounts of organic matter present in seedlings which had developed, in carbon-dioxide-free air, either in light or in darkness. In several experiments with *Raphanus* and *Zea,* of various ages up to three weeks, no significant and consistent differences were observed between the different light treatments. In similar experiments with wheat, the loss of dry weight was somewhat greater, and the content of water-soluble carbohydrates somewhat less, in plants exposed to a low light intensity than in those grown either in full sunlight or in darkness (175). Shirley suggested that the results of Lubimenko and Karisnev may have been due to temperature differences among the various lots of plants.

e. Suppression of Photosynthesis by Intense Illumination. It has been observed by a number of investigators that under conditions of intense illumination the rate of apparent photosynthesis may be markedly reduced. Where this reduction is great enough to result in a net liberation of carbon dioxide or uptake of oxygen, direct evidence of an alteration of the respiration rate is provided.

In a culture of *Hormidium flaccidum* which had been grown in continuous illumination of low intensity, van der Paauw observed in strong light (presumably furnished by a 150-watt lamp at about 14 centimeters) an oxygen consumption two to four times as great as in darkness. The same result was found repeatedly with this particular culture but could not be obtained at a later date with other cultures. That the cells were capable of assimilation was shown by an experiment at low intensity.

Föckler, who determined oxygen by the Winkler method at hourly intervals, reported a similiar effect for fronds of *Trichomanes radicans* in bright sunlight. The rate of oxygen consumption increased with time of illumination up to about two hours, after which it remained relatively constant for at least two more hours. The maximum rate in light was four to six times that in the preceding

dark period. In darkness following exposures of two to four hours the respiration rate fell, at first rapidly and then more slowly; it had not quite returned to the original dark level by the fifth day but had done so by the fourteenth day. Following a one-hour exposure, on the other hand, a further increase in respiration was observed during the first hour of darkness, after which the rate decreased. Although the cells presented an abnormal appearance and a lighter color for a time after the irradiation, they had not been killed; after several days the photosynthetic capacity (in light of moderate intensity) returned. Similar results were found also with portions of thalli of *Laminaria digitata*.

Using the Warburg manometric technic with excellent temperature control, Myers and Burr measured the oxygen uptake by suspensions of *Chlorella vulgaris, C. pyrenoidosa* and *Protococcus* sp. over a wide range of light intensities provided by incandescent lamps. At the highest intensities studied (39,000 foot-candles) the rate of oxygen consumption was as much as three times as great as in the dark. The amount of stimulation, which was less at lower intensities, was relatively independent of the carbon dioxide concentration of the suspending medium, at least within the limits studied, as well as of the cultural history of the cells.

These authors investigated also the time course of the oxygen exchange during exposure to a series of light intensities. On first illumination, oxygen was evolved in all cases; but within several minutes, at intensities of 4,000 foot-candles and greater, the rate of oxygen production began to diminish; at intensities greater than about 12,000 foot-candles, it became negative. On prolonged exposure this absorption of oxygen continued at a fairly constant rate, both the magnitude and duration of absorption depending on the intensity. After one to a few hours the rate of oxygen consumption became smaller, finally approaching zero. At the stage when the decreased rate of oxygen uptake commenced, visible bleaching of the cells occurred; the cells were irreversibly injured at this point, and return to darkness did not result in recovery of the normal respiration rate. This stage appeared to set in after a definite volume of oxygen had been consumed, regardless of the rate of uptake. If the algae were exposed to the radiation for only a short interval and then placed again in darkness, the normal respiration rate was regained after a time. Immediately after turning off the light, how-

ever, there was a considerably higher rate of oxygen uptake which was the more persistent the longer the previous exposure had been.

f. Suppression of Photosynthesis by Prolonged Sojourn in Darkness. Kniep reported data from an experiment in which two thalli of *Fucus serratus* were kept in darkness during a period of five months. The plants appeared perfectly healthy at the end of this time, although frequent measurements of the oxygen consumption in darkness showed a continued decrease of respiration, until at the end it amounted to only about one-fifth of the value at the start. The respiration was then measured in diffuse daylight and was even slightly higher than the original level of five months earlier; that is, it showed an approximately 400% increase over the dark rate measured three days before. The thalli were then returned to darkness for two days, after which the respiration of one was measured in darkness, that of the other in light. In darkness there was still apparent about 75% of the stimulation induced by the previous illumination, whereas the second thallus, measured in light, showed a still further increase of 40% over the first light determination.

Föckler kept plants of *Potamogeton lucens* in darkness for 10 days, by the end of which time most of the chlorophyll had disappeared. About 80% of the cells were still viable, as indicated by a plasmolysis test, and the dark respiration was stated to be normal. On illumination by sunlight the oxygen consumption was one and one-half times that in the preceding dark period; on replacement in darkness the respiration returned approximately to the original value.

Indirect evidence, photosynthesis occurring. In addition to the information obtained from experiments in which photosynthesis is experimentally suppressed, circumstantial evidence may be derived from several types of experiments in which the assimilation is allowed to proceed normally. It is under precisely such conditions, of course, that information concerning respiratory changes is of greatest significance for assimilation studies. Indirect evidence of the kinds here considered must of necessity lack conclusiveness, inasmuch as a multiplicity of related or unrelated reactions and physiological processes may influence the over-all changes which are measured.

No attempt will be made in the following discussion to review the vast literature on photosynthesis; a number of citations illustrative of the various lines of evidence should suffice.

a. Evidence from Inconstancy of Photosynthetic Rate at High Light Intensities. In the preceding section there have been considered as direct evidence the cases in which the apparent respiration in light was greater than the respiration in darkness. There are, in addition, a large number of reports of a decreased (although still positive) rate of apparent photosynthesis in light of high intensity.[3] Although such data must be regarded as quite indirect evidence, it seems not improbable that some of the instances cited below differ from those described in the preceding section only in the degree of the respiratory stimulation.

In general two types of information are available: *a*) from experiments in which the photosynthetic rate has been measured as a function of the light intensity at high intensities, and *b*) from experiments in which the time course of photosynthesis has been followed at high intensities. Decreased rates of apparent photosynthesis with increasing light intensities have been observed (73, 103, 125, 140, 141, 195, 226, 281), as well as reduction of photosynthetic rate with time of exposure to light of high intensity (6, 19, 47, 122, 194, 195, 211, 226, 238, 275, 322).

In recent years some workers have referred to these phenomena as "solarization" effects, although the term as introduced by Ursprung in 1917 was used only in connection with starch formation and disappearance.

In general, it may be said that these effects of high intensities are more pronounced in shade leaves or plants than in sun leaves. The sensitivity of many plants can be increased also by shading or darkening for some time prior to the experiment.

Whether the observed diminution of apparent photosynthesis is due to a decrease in the true photosynthetic rate or to an increase in respiration can not be decided with certainty at the present stage of our knowledge. Possibly both factors may be of importance in individual cases. The data of Myers and Burr are consistent with the view that with increasing intensities, there occur a simultaneous progressive inhibition of photosynthesis and a progressive increase of the light-induced oxygen absorption.

[3] Lest a misleading impression be created, it should be mentioned that in a considerably larger number of experiments the rate of apparent photosynthesis has been found to be quite constant over a wide range of light intensities. While these data in themselves bespeak the absence of any effect of light on respiration, the question always remains whether the constancy would be found also at intensities still higher than those studied.

A number of suggestions as to the possible internal causes of decrease in the true photosynthesis have been advanced: stomatal closure affecting carbon dioxide diffusion, photic or thermal fatigue of the assimilation mechanism, photodestruction of chlorophyll, accumulation of assimilates, and reduction of the functional assimilation surface through phototaxis of the chloroplasts. The diversity of experimental conditions and types of biological material with which the phenomenon has been observed would appear to rule out each of these possibilities as the sole cause of the effect, although all of them may play a rôle in particular instances. It should be mentioned also that in many of the experiments cited the significance of the observed results may be obscured by methodological uncertainties (see 80). For attempts to relate these effects more intimately to the photosynthetic process, reference may be made to Gaffron (98) and to Franck and French.

On the other hand, it can not be denied that these results strongly resemble those, mentioned in the preceding section, in which an increased rate of respiration could be demonstrated directly, the difference appearing to be merely one of degree.

b. Evidence from the Respiration Rate in Darkness after a Period of Illumination. Borodin (29) seems to have been the first to note an increase in the rate of dark respiration, subsequent to a period of illumination, as compared with that preceding it. Rischawi suggested that Borodin's results could be explained, in part at least, through a physical absorption of carbon dioxide in light with subsequent release in darkness. In this connection, although its significance is not clear, mention should be made of the interesting finding that more carbon dioxide could be extracted by a vacuum from leaves (both green and chlorophyll-deficient) after a period of illumination than after a stay in darkness (269).

The criticisms of Rischawi appear to have been satisfactorily refuted by Borodin (30) who confirmed and extended his earlier observations. The general findings were that detached shoots of *Crataegus oxyacantha, Spiraea opulifolia* and *Larix europaea* exhibited a marked increase in rate of respiration, whether measured as carbon dioxide production or as oxygen absorption, following a few hours exposure to sunlight. A greater effect was induced by direct than by diffuse light and much greater by red light than by blue light, although the intensities presumably were not equalized

in this comparison. The stimulation was absent, or at most very slight, if carbon dioxide were excluded during the exposure.

Aereboe, who measured carbon dioxide production in darkness by shoots of yellow lupine immediately after excision, found that the rate was markedly influenced by the illumination conditions to which the plants had been subjected during the preceding few days. After a period in bright daylight the respiration was much higher than following a stay in semidarkness. The conditioning of the plants to low or high respiration levels could be reversed by changing from one light environment to the other.

According to Matthaei, the dark respiration rate of detached leaves of *Prunus laurocerasus* after a period of illumination of fairly high intensity was several times greater than that preceding the exposure. Using partly etiolated leaves of *Beta vulgaris,* Meyer and Deleano noted a marked increase in the rate of dark carbon dioxide production after several hours exposure, in the presence of 2% carbon dioxide, to visible electric light of about one-fourth full solar intensity. If carbon dioxide was not provided, only a small, possibly insignificant, effect was found.

Pantanelli (1914) stated that in seven species of marine algae the rate of carbon dioxide evolution in darkness was considerably greater after a period of bright light than after a sojourn in weak light, whereas oxygen absorption usually did not vary greatly under the two circumstances. Hence, a much higher respiratory quotient was found in the algae exposed to the higher intensity. *Valonia utricularis* formed an exceptional case, inasmuch as light treatment occasioned very little change in the carbon dioxide production. The dark respiration of *Enteromorpha compressa* was observed to be about twice as great following a day's exposure to direct sunlight as it was after a day in subdued daylight (120). Spoehr and McGee reported measurements of the carbon dioxide production of detached leaves of sunflower and bean in darkness preceding and following periods of Mazda illumination of a few hours' duration. Of five experiments, one showed a marked increase after illumination, two showed appreciable decreases, while in the other two there were no significant differences. Waller observed a transient acceleration of the carbon dioxide production of detached leaves in darkness after a period of rapid photosynthesis. According to Harder (122), a period of exposure to electric light of 14,000 to 16,000 meter-candles increased the dark respiration of *Fontinalis* by 11% to 61%.

In several experiments with *Hormidium flaccidum,* van der Paauw consistently found that respiration subsequent to irradiation, presumably by a 150-watt incandescent lamp at 13 centimeters distance, was greater than that preceding the light period. Immediately following the illumination the rate of oxygen consumption was increased as much as two-fold; subsequently it declined, rapidly at first, and then more slowly, reaching the original level in about two hours. Parija and Saran observed that the dark respiration of detached *Aralia* leaves was increased by a short exposure to radiation filtered through glass and water, from a 60-watt lamp at 10 inches distance. The stimulation presumably amounted in some cases to 100% or more. An exposure of seven and one-half minutes was stated to result in as large an increase as that for two hours. The data presented indicate that violet light was considerably more effective than white or blue light said to have been of equal intensity; red light was without influence on the respiration. Similar effects were found both with green leaves and with chlorophyll-poor albino leaves, but in either case only with leaves which had been detached from the parent plant for several hours. It was shown also that none of the leaves used was capable of photosynthesis under the conditions of illumination and age at which maximal respiratory stimulations were found.

Mitchell found the dark respiration of entire soybean plants considerably higher following a day of illumination than after an equal period of darkness. Large increases in respiration rate following exposure to sunlight were reported also by Montfort. Stålfelt (281) observed that a period of illumination at 16,000 lux occasioned increases of 18% to 144% in the dark respiration of several species of lichens.

Of 12 species of aquatic plants studied by Gessner (103), six showed an increased oxygen consumption following 40 minutes exposure to electric light of 40,000 lux, whereas six showed a decrease. In view of the large experimental error and the technical difficulties encountered, the significance to be attached to these results appears to be uncertain. Further experiments showed that consistent results could be obtained only when due consideration was had for the duration of the irradiation and of the preceding dark period (104). Following 60 to 65 hours of darkness, exposures of two or four hours to electric light of 40,000 lux resulted in respi-

ratory increases up to 50%. A 30-minute illumination was insufficient to produce consistent stimulations. The increases observed are to be regarded as minimal effects, since, as Gessner has pointed out, the aquatic plants used are able to accumulate, in their intercellular spaces, considerable quantities of oxygen (produced by photosynthesis) during the illumination period; subsequent utilization of this stored oxygen diminishes the apparent rate of respiration. Experiments with filters and with a mercury arc source indicated that the respiratory stimulation was produced by both visible and ultra-violet radiation. Increases as large as 94% were found after the ultra-violet treatment, but the intensity data given are insufficient to permit a comparison of the effectiveness of the two spectral regions. The increased rates of oxygen consumption persisted in darkness as long as the experiments were continued (two to five hours).

Smith (275), in a study of photosynthesis by *Cabomba,* stated that the dark respiration following a period of active assimilation was always higher than that preceding the illumination. Similar results were obtained by van Hille. Neubauer observed higher rates of dark respiration in leaves detached after a bright day than in those removed following a rainy day.

Föckler, who measured the oxygen consumption by several species of aquatics before and after an exposure of one to three hours of daylight or electric light, found in all cases a respiratory increase. This stimulation amounted to 24% to 229%, and in some cases persisted during at least four hours of darkness subsequent to the illumination. Carbon dioxide production by *Usnea dasypoga* and *Ramalina fraxinea* in darkness immediately after a 10-hour light period averaged about 54% higher than that preceding the irradiation. With intensities of electric light up to 48,000 lux the stimulation was substantially independent of the intensity (283).

Mothes, Baatz and Sagromsky reported that the rate of oxygen consumption by chlorophyllous algae and tissues of higher plants was greater after a period of illumination than in comparable dark controls. This stimulation was smaller at low carbon dioxide concentrations and was elicited only by long light periods. In several other experiments the rate of dark oxygen uptake by *Chlorella pyrenoidosa,* measured with the dropping mercury electrode, was considerably greater immediately following a period of illumination, even of quite low intensity (232).

Gaffron (96) reported an experiment in which the dark respiration of *Scenedesmus basiliensis* was measured before and after a ten-minute illumination (intensity presumably about 10,000 lux). Following the exposure the rate of oxygen consumption was 20% higher, the rate of carbon dioxide production 39% lower, than that preceding it. Correspondingly, the respiratory quotient was reduced from 1.80 to 0.92.

Bode, using the manometric technic, investigated the influence of illumination on the subsequent dark respiration of *Fontinalis antipyretica*. Prior to the measurements the plants were cultured either in red or in blue light of about 1,200 lux. Following a 24-hour dark period, at the end of which the respiration was determined, a two-hour exposure to red or blue light of approximately 10,000 lux was given, and then the respiration again measured in darkness. The results, which were very consistent in a series of experiments, showed a 73% stimulation by blue light in the "blue-cultured" material and 66% for the "red-cultured" plants. Red light resulted in 40% and 48% stimulations, respectively, for the two types of material.

The rates of carbon dioxide production by entire *Pistia* plants in darkness before and after a 12-hour period of exposure to radiation, filtered through water and glass, from a 1,000-watt lamp at about one foot distance were determined by Ranjan (244, I). In darkness after illumination the respiration rate increased, usually only after some hours, to a maximum and then decreased again. The apparent delay in attainment of the maximum rate was attributed to experimental difficulties. The maximum increases over the preceding dark rates in four experiments, performed at 40°, 35°, 27° and 20.5° C., were approximately 30%, 45%, 28% and 10%, respectively. Evidence of a respiratory stimulation was obtained also in some similar experiments with detached leaves of *Eugenia jambolana* (242, 244, II).

The same investigator studied also the influence of radiation from a mercury arc on the respiration of detached leaves of *Eugenia* (244, IV). After a total of 18 minutes exposure to the unfiltered radiation the rate of carbon dioxide evolution in darkness was decreased by about 40%. Three-minute irradiations at the same intensity had little or no effect, whereas, curiously enough, exposures for the same length of time at one-fourth the intensity resulted

in decreases in the subsequent respiration. Four hours of exposure to the arc radiation filtered through glass caused a dark stimulation of approximately 64% in an experiment performed at 25° whereas at 33° a decrease in the subsequent dark respiration was noted. After six hours of violet light, obtained by means of a methyl violet solution filter, the rate of dark carbon dioxide production was unaffected in one experiment but appreciably decreased in a second.

In contrast to the numerous observations of increased respiration following irradiation are those of a limited number of experiments with *Aspidistra,* which revealed a much smaller rate of dark carbon dioxide production after an illumination period (100). In view of the inconstancy of the respiration rates in these, as well as other experiments performed at the same time, the validity of the results appears questionable.

In recent years several workers, using improved technics, have observed irregularities in the rate of gas exchange immediately after a transition from darkness to light, or *vice versa* (8, 9, 21, 81–83, 98, 180, 181). Numerous suggestions of more or less similar "anomalies" are to be found also in the older literature on photosynthesis. The significance of these results is not entirely clear, as yet; in any case, the effects are of much smaller magnitude than are those described above.

On the other hand, many investigators who have measured, in connection with studies of photosynthesis, the respiration in darkness before and after illumination have never noted after-effects of the irradiation. In view of the possibility that many as yet unappreciated factors may influence the respiration response to light, it seems reasonable to expect that either positive or negative results could be obtained if such factors were not controlled. For this reason the reviewer feels that, of equally careful experiments, those which demonstrate positive effects are of much greater evidential value.

Some additional lines of information should perhaps be included in this section, although, admittedly, they may prove to have little bearing on the question concerned.

Saikewicz, who measured the carbon dioxide production by intact roots of maize plants, found a greater respiration rate during the day than at night; a decrease in rate was noted also when the plants

were moved from bright sunlight into diffuse light. Similar experiments have indicated that a light-induced periodicity in the root respiration occurred only after the plant had been kept for some days in conditions of low light intensity (3).

A number of workers have compared the respiratory activities of plants cultured under different intensities of light. In *Teucrium scorodonia,* Rosé found the highest rates of carbon dioxide production, on a fresh weight basis, in plants grown at intermediate intensities; this was true also for older plants of *Pisum sativum,* whereas among younger plants those cultured at the highest intensity showed the greatest respiratory rate. The respiration rate, on a fresh weight basis, was considerably less in partially etiolated leaves of *Raphanus sativus* which had developed in light of low intensity than in those grown in higher intensities (43).

Hicks and Panisset, who cultured *Lemna* at various intensities of 350 to 1,400 foot-candles, reported that the rate of carbon dioxide production per frond was greater the lower the light intensity. In similar experiments with *Lemna minor,* the respiration rate, calculated on the basis of leaf area, increased with increasing light intensity of the previous culture period, but on a dry weight basis the reverse was true (319). According to Chia, anthocyanin-containing plants of *Amaranthus* which had been grown under intensities of artificial light of 31, 220 and 431 foot-candles showed relative respiration rates of 100, 138 and 163, respectively, as compared on a fresh weight basis. Sargent found the rate of oxygen uptake per unit volume of *Chlorella pyrenoidosa* cells cultured at high light intensity to be nearly twice that of cells grown at low intensity. The difference in rate of carbon dioxide production was considerably less, so that the average respiratory quotient for the "sun" plants was 1.1, whereas that for the "shade" plants was 1.6. Iuracec compared the carbon dioxide production by leaves of bean plants which for some days previously had been cultured in direct sunlight or in shade. The respiration of the sun leaves was 80% to 90% greater when calculated on the basis of area, fresh weight or water content, 40% greater on a dry weight basis, and 106% greater per leaf.

c. Evidence from the Compensation Point. The term "compensation point" was introduced into plant physiology by Plaetzer in 1917 to designate the light intensity at which assimilation and respi-

ration rates compensate each other with a resultant zero gaseous exchange. The compensation point as thus defined has proved to be an extremely valuable concept, especially in ecological problems. It may be mentioned parenthetically, however, that it lacks precision to the extent that the material under consideration is not definitely circumscribed. Thus, a chloroplast, a cell, a leaf and a shoot, as well as the entire plant itself, will in all probability have quite different compensation points. Further complication arises through the possibility, occasioned by differences between respiratory quotient and photosynthetic quotient, that under some conditions there may exist separate compensation points for oxygen and for carbon dioxide. Obviously, the compensation point will be influenced by all those factors which affect either photosynthesis or respiration. Variations of the compensation point thus afford evidence of changes in one or both of these processes.

There is abundant evidence that the compensation point is influenced greatly by the previous illumination intensity to which a plant has been exposed. In some cases it has been possible experimentally to effect more or less marked alterations of the compensation point by culturing in light of different intensities (62, 76, 121). The compensation point is higher after a regime of more intense illumination. Numerous studies have demonstrated, furthermore, that the compensation point of sun plants or sun leaves is, in general, higher than that of shade plants or shade leaves (*e.g.,* 33, 34, 76, 121, 129, 177, 260, 280a).

From such evidence alone it is, of course, not possible to definitely ascribe the compensation point differences either to an altered respiration rate or to an altered assimilation rate. A number of investigators have shown, however, that the respiration rates of shade plants or shade leaves are, by and large, appreciably smaller than those of corresponding sun plants or sun leaves (*e.g.,* 4, 34, 101, 126, 141, 177, 189, 260, 280a). (Compare also the several examples, given in the preceding section, of lower respiration rates in plants cultured under low light intensities.)

It seems altogether likely, therefore, that the influence of illumination conditions on the compensation point is due, at least in part, to an effect of light on the respiration rate.

A quite different type of indirect evidence was utilized by Noddack and Kopp, who worked with *Chlorella pyrenoidosa.* From a

consideration of the relationships between the rate of apparent photosynthesis and the light intensity at different temperatures, it was calculated that the respiration was diminished in light, under the conditions employed (15-minute exposure to low intensity light of λ6500 Å).

EFFECTS OF NON-VISIBLE RADIATION

Infra-red Radiation

With relatively few exceptions investigators have recognized the possibility of an indirect temperature effect due to absorption of infra-red radiation and in most instances have made some attempt to eliminate it. There appears to be no evidence of direct specific infra-red effects.

Ultra-violet Radiation

Cook and Stephenson measured the oxygen consumption by *Escherichia coli* immediately after exposure to radiation from a quartz mercury arc. In the presence of glucose, acetate or lactate, the total amount of oxygen absorbed for a given amount of substrate was uninfluenced by prior irradiation in dosages great enough to reduce the number of viable organisms to less than 0.3% of the control. The initial rate of oxygen uptake, however, was decreased by approximately 58% in the irradiated cultures. With formate as substrate, the initial rate following exposure was only about one-tenth, and the total amount of oxygen absorbed was only about one-half of that of the control.

Giese studied the influence of ultra-violet radiation (consisting chiefly of λ 2537 Å) on the oxygen uptake of the luminous bacterium *Achromobacter fischeri,* using the Warburg technic (105). After small dosages of radiation (of the order of 1,000 ergs/mm.^{2}), the respiration rate was unaffected for several hours but eventually showed a decline. Larger dosages (up to 64,000 ergs/mm.^{2}) were followed by earlier and more pronounced decreases in the rate of oxygen absorption, the effects being proportional to the dosage. Since the respiration (in presence of glucose and/or peptone) was affected similarly whether the cells were irradiated in the presence or absence of the substrate and as no effect was produced by irradiation of the medium alone, it was concluded that the radiation acted directly upon the organism. The relationship found between concentration of glucose supplied and rate of oxygen uptake suggested

that the glucose-activating dehydrogenases were selectively inactivated. Giese reported that if the cultures were shaken in absence of nutrients for long periods prior to irradiation, a respiratory stimulation could be observed following exposure (106). Thus, after an irradiation of two and one-half minutes at about 70 ergs/mm.^{2}/sec., the rate of oxygen consumption was approximately 40% greater than that of the control; a 10-minute exposure resulted in an increase of about 100% but this was not maintained for as long a time. Cells irradiated shortly after washing from nutrients did not manifest the ultra-violet-induced stimulation but showed a decline in respiratory rate, as previously found.

The influence of ultra-violet radiation on respiration and fermentation of yeasts has been studied by a number of investigators. A considerable portion of these experiments, performed with impure cultures, in complex media, by inadequate technics or without regard for effects on growth and viability, are very difficult to evaluate.[4]

Very striking claims of increase in fermentation rate following irradiation have been made (65–67, 87, 169). It was increased 22% by exposure to radiation of λ 2,000–2,500 Å for five minutes at 15 centimeters from a quartz mercury arc of 1,000 Hefner candles intensity (35), and small transient increases in the rate of anaerobic carbon dioxide production were noted after short periods of irradiation by a quartz mercury arc (329). Longer exposures resulted in a slight inhibition. Hinrichs also found short exposures to result in increased fermentation, whereas more prolonged irradiation was inhibitory. Others have concluded from their experiments that ultra-violet irradiation resulted in an increased fermentation rate and higher fermentation efficiency (221, 222), but these conclusions have been severely criticised (292, 326).

Gronchi measured carbon dioxide production during and after exposure of glucose suspensions of *Saccharomyces cerevisiae* to a quartz mercury arc, using filters to isolate radiation of 2,200–3,800 Å and 3,650 Å (111). During the exposure the fermentation rate was greater than in the untreated control, but following the treatment the rates dropped to values much lower than that of the control. The inhibition produced by the 2,200–3,800 Å radiation was evident even 48 hours later.

Others have reported that short exposures to ultra-violet radiation stopped fermentation (186, 187), or decreased it (1, 278,

[4] Much of the earlier literature has been critically discussed (292, 326).

292, 293). No evidence of stimulation was ever observed by these authors. A temporary decrease, possibly followed by a slight increase, in rate of alcohol production, was observed on one occasion (10).

The influence of a number of spectral regions, obtained with a quartz mercury arc in conjunction with various filters, on the anaerobic carbon dioxide production by baker's yeast, has been studied (248). The measurements, made during the second hour of irradiation, showed wave-lengths longer than 3,000 Å to be without effect on the fermentation rate, whereas marked inhibition was produced by radiation between 3,000 and 2,500 Å. The inhibition was unaccompanied by general injury to the cells, so far as could be determined from the stainability by methylene blue.

Oster measured the oxygen consumption of yeast immediately after exposure to various ultra-violet lines of the mercury spectrum and observed no effect on respiration unless the irradiation had been sufficient to damage the cells, in which case the oxygen uptake was decreased. Tang found that exposure of *Saccharomyces wanching* to the radiation (of unspecified intensity) from a quartz mercury arc decreased the subsequent dark respiration, the degree of inhibition increasing with the duration of the irradiation period. The aerobic respiration of *Saccharomyces cerevisiae* was stated to be relatively unaffected by ultra-violet radiation of wavelength 2,650 Å (5). A 50% increase in oxygen uptake due to ultra-violet raying has also been observed (286).

The problem of stimulation of yeast respiration by ultra-violet irradiation was studied also by others, using the manometric method (85). In several experiments exposure to radiation of unspecified intensity from a quartz mercury arc increased the subsequent respiration rate by amounts up to 157% above the untreated control. Under the conditions employed the maximum stimulation occurred after five minutes of irradiation; exposures of 10 minutes or longer depressed the rate of oxygen consumption below that of the control. Increases in respiration were not accompanied by more rapid cell reproduction; rather, the raying resulted in a retarded multiplication rate. Evidence was obtained also that the respiratory stimulation persisted for at least 24 hours after treatment, although these experiments are less clear-cut. Additional study showed, however, that the results could not be obtained consistently; in many cases

depression of respiration was observed under the conditions which had originally produced stimulations.

The effect of ultra-violet irradiation on oxygen uptake of *Saccharomyces cerevisiae* has been investigated also by Giese (106). A Sterilamp, emitting principally λ2,537 Å, was used as the source; the incident intensity was approximately 70 ergs/mm.²/sec. The relatively low rate of respiration of washed cells suspended in buffer solution was markedly increased after short exposures. Thus, in one experiment treatments of 1.25, 5 and 10 minutes, respectively, resulted in increases of approximately 20, 80 and 200%. The increased rate of oxygen uptake, which, incidentally, was never greater than that of non-irradiated sugar-fed cells, was maintained practically constant for at least two hours and in other experiments was evident at least 12 hours later. An exposure of 20 minutes gave an even larger initial stimulation but was not maintained. The reproductive capacity of the cells was very greatly diminished by even the 10-minute irradiation.

Cells furnished with glucose in concentration high enough (>0.1%) to produce the maximal rate of oxygen uptake in the controls, showed no stimulation after ultra-violet exposure but, instead, exhibited a respiratory rate smaller than that of the non-irradiated culture. Stimulation by ultra-violet was elicited, however, in the presence of suboptimal amounts of glucose (0.05%).

Apparently inconsistent results were obtained on the addition of glucose to cultures which had been irradiated some hours earlier in its absence; in one case the sugar produced a marked increase in rate of oxygen consumption, whereas in another experiment no effect was observed. The cause of this discrepancy is not evident; it would appear that the factors governing the respiratory response to radiation are not entirely appreciated, and this probably accounts for the discordant findings of various investigators. It is interesting to compare the results of Giese with those of Rubenstein on the effect of visible radiation on respiration of *Sarcina lutea,* which have been mentioned above. In the work of the former the possible influence of the temperature was not investigated. Giese concluded that the respiratory stimulation induced by ultra-violet irradiation is not due, in any considerable measure, to the liberation of respirable substrate from the cells, but rather to the production of catalytically active substances which enhance the capacity of the starving cell to

oxidize its contents. In experiments with the mycelium of *Neurospora crassa,* no evidence of ultra-violet stimulation was observed.

Pasinetti and Grancini reported that several minutes exposure to ultra-violet radiation had no marked effect upon the subsequent gaseous exchange of *Corticium rolfsii, Sclerotium delphinii* and *Alternaria brassicae.*

Bonnier and Mangin (27) found different respiratory quotients for several green plants when measured in darkness and when measured during exposure to ultra-violet radiation obtained from sunlight by means of filters. It is possible, as the authors believed, that some photosynthesis was taking place so that the results are not at all conclusive but merely suggestive of a possible effect of ultra-violet radiation on respiration. Masure reported two experiments in which the oxygen uptake of etiolated pea seedlings was measured before, during and after exposure to a band of radiation, of unmeasured intensity, from about 3,334 to 3,650 Å. Certain large irregularities in the results are attributed by the author to heating effects, and it appears possible that the observed respiratory stimulations may in reality have been due to similar causes.

Wynd, Fuller and Reynolds subjected plants to successive short daily doses of mercury arc radiation minus the infra-red longer than 1.4 μ, in addition to the normal solar illumination. In one experiment the carbon dioxide production of tomato plants on the day following five weeks of daily 10-minute exposures to radiation (lacking the ultra-violet shorter than 2,894 Å) was 31% greater than that of the controls; the treated plants also showed a higher catalase activity, whereas oxygenase and peroxidase activities were practically the same as in the controls. On the next day no marked respiratory stimulation could be demonstrated, but the catalase activity was still quite high. Plants which had received radiation including the shorter ultra-violet, exhibited no appreciable increase in respiration, although the catalase activity was even greater than in the plants mentioned above. A somewhat similar experiment with beans gave quite different results. In the irradiated plants, all of which showed injury, the peroxidase activity was very markedly increased over that of the controls, whereas the catalase activity and respiration rates were not consistently different in the two sets.

In a second experiment with tomatoes, radiation, including the shorter ultra-violet of much higher intensity, was supplied in 15- or

30-minute daily doses over a four-day period. Evidence of respiratory stimulation persisting for at least four days after cessation of irradiation was obtained, but interpretation of the results is complicated by the marked injury suffered by the plants. In general, the peroxidase activity of these plants was higher, the oxygenase activity lower than in the controls; the catalase activity which on the day after termination of the irradiation was lower than in the controls, increased day by day until on the fourth day the value was much higher than in the untreated plants.

Chia observed that exposure of *Amaranthus cordatus* to an unscreened Cooper-Hewitt mercury arc resulted in increased oxygen consumption as compared with unirradiated control plants. Fifteen- and 30-minute exposures gave increases of 10% and 12% respectively, whereas an hour's treatment produced only a 4% increase. Following daily exposures of three to five minutes, continued over a period of three weeks, respiratory stimulations of 20% to 23% were found.

In the experiments of Gessner (104) an apparent decrease in oxygen consumption was observed during exposure to long wavelength ultra-violet radiation, but in this case, too, it is quite likely that the ultra-violet or the small amount of red light which was also present may have permitted some photosynthesis.

The results of Föckler on excised roots and of Ranjan with green leaves have been described in preceding sections.

Further use of ultra-violet radiation as a tool would appear to be rather promising in view of the finding that by such irradiation photosynthesis of *Chlorella* could be entirely inhibited for at least seven hours without any appreciable effect on the dark respiration (7).

In summarizing briefly the results obtained with ultra-violet it may be said that, so far as the respiration of bacteria and yeasts is concerned, such radiation has been found to be either inhibitory or without influence; no claims of stimulatory effects have yet been made. The available reports dealing with yeast fermentation are approximately equally divided between claims of stimulations and of inhibitions. The best work on higher plants indicates that more or less clear-cut stimulations may be induced by irradiation. The findings from the experiments in which long periods of treatment have been employed are difficult to assess, however, since many secondary effects must be taken into consideration.

X-Radiation

The influence of x-rays on respiration and fermentation of aqueous suspensions of baker's yeast has been studied, and manometric measurements made 30 to 60 minutes after exposure showed no significant differences between treated and control cultures (317). Oxygen consumption of *Staphylococcus aureus* also was unaffected by x-irradiation, even though the reproductive capacity of the cells was greatly diminished by the treatment. Similar results were obtained with suspensions of beer yeast (318).

According to von Euler, the rate of oxygen consumption by yeast was increased about 40% after x-irradiation, but returned to normal on the addition of sodium arsenate. The increase in rate was partially nullified by addition of yeast extract, which however, had no influence on respiration of normal cells.

Schneider found the fermentation rate of yeast reduced by x-irradiation (262), but in the presence of dyes no influence could be demonstrated (263). The results of Lossen and Schneider were rather inconclusive. According to Zeller, the rate of anaerobic carbon dioxide production by yeast following x-irradiation decreased at first, then increased and finally returned to the level of the unexposed control. His results suggested that misleading conclusions might be reached unless care were taken to observe the entire course of events subsequent to irradiation.

Gronchi observed increases of the order of 10% to 40% in rate of yeast fermentation, both during and after exposure to x-rays (110, 112). The magnitude of the stimulation was said to be proportional to the intensity of the radiation within the range employed (dosages of 300 to 2,000 roentgen units during a period of 45 minutes). Greater effects were produced by shorter (average = 0.16 Å) than by longer (average = 0.37 and 0.55 Å) wavelengths. Others have reported 5%, 20% and 35% increases in rate of oxygen uptake following x-irradiation of yeast suspension for 15, 30 and 60 minutes, respectively (85).

An increased rate of gaseous exchange following x-irradiation of *Corticium rolfsii, Sclerotium delphinii* and *Alternaria brassicae* has also been observed (228).

Petry measured the gaseous exchange of pea and wheat seedlings during the 24-hour period immediately after a 15- to 30-minute exposure to x-rays. Both carbon dioxide production and oxygen

consumption were reduced by about 10% in comparison with the untreated controls. Five to eight days later the respiration was only 40% less than that of the controls, even though marked growth derangements were manifest. The carbon dioxide production of *Helianthus annuus* seedlings during a nine-day period subsequent to x-irradiation of the seeds was investigated and both the respiratory rate and the growth rate, as compared with controls, were found to be decreased (142).

Francis measured the rate of carbon dioxide production at 6, 28 and 52 hours after exposure of 24-hour-old wheat seedlings to various dosages of x-rays up to 13,560 roentgens. The rate of respiration per plant was depressed in all cases except for the earliest measurement of the plants receiving the smallest dosage (565 roentgens), which showed a small stimulation. The extent of the inhibition was dependent upon the dosage. Growth was also depressed by the treatment so that, in comparison with the controls, the exposed plants exhibited a slightly greater respiratory rate on the basis of linear growth of the seedlings, a somewhat lower rate on the basis of dry weight and, at the earliest measurement, a greater respiration on the basis of fresh weight.

Chesley exposed 18-hour-old wheat seedlings to doses of γ- and x-rays sufficient to decrease the subsequent growth by as much as 40%. Growth, as measured by fresh weight, was markedly reduced even in the first few hours after treatment, whereas the oxygen consumption (measured manometrically) per plant was not significantly different from that of the controls. Respiration expressed on unit weight basis was, therefore, greater in the irradiated seedlings. During the period from 24 to 48 hours after exposure the oxygen uptake closely paralleled the growth: the respiration per plant was lower in the treated seedlings, but on a weight basis was nearly identical in the two sets. In an experiment in which the seedlings were kept at 6° during the 48 hours immediately following irradiation, no growth occurred, and at the end of this period the respiration (measured at 26°) was equal in treated and control plants whether calculated per seedling or per gram. These results indicate that the effects on respiratory rate are expressions of the decreased growth rather than its cause, and Chesley concluded that the primary influence of the radiation is not upon the respiratory mechanism itself.

Shull and Mitchell obtained indications of increased sugar content and respiration rate of corn seedlings after irradiation with small dosages of short wavelength x-rays.

Carbon dioxide production of sprouted bulbs of *Narcissus tazetta* has been measured at various intervals following exposure to an x-ray dosage of 3,500 roentgens. The results of separate experiments were rather inconsistent, and no general conclusion appears to be warranted. Thus, of seven sets of plants measured one-half hour after exposure, the carbon dioxide output on a fresh weight basis was less than that of the controls in four, greater in two, and equal in one. Of three other sets measured five hours after irradiation, one showed an increase, one a decrease, and one no change in the rate of carbon dioxide production as compared with the controls. Results at later periods were complicated by differences in the weight and height changes.

Bersa determined the rate of oxygen consumption by one-centimeter long root tips excised at intervals subsequent to exposure of soaked *Vicia faba* seedlings to x-rays. Roots excised within less than an hour after treatment showed a slight respiratory stimulation; at six hours no difference was found between irradiated and control roots. After intervals of one, two or three days the irradiated roots were markedly shorter and thicker than those of the normal seedlings, and the rate of oxygen uptake, on a fresh weight basis, fell ultimately to about one-half that of the controls.

To recapitulate the effects of x-radiation, no influence on bacterial or yeast respiration has been reported. With the exception of the somewhat uncertain results of Schneider, yeast fermentation has been found to be stimulated to some degree. The findings with higher plants are in fairly good agreement, generally showing decreases in respiration, although small and transient stimulations may be produced by low dosages. The inhibitions, at least, appear to be related to more direct influences of the radiation upon other physiological processes rather than primarily due to action upon the respiratory mechanism.

γ–*Radiation*

As the studies dealing with the effects of γ–radiation on respiration, fermentation and metabolism of plants have been admirably reviewed in a monumental treatise (285), they need not be considered here.

Hertzian Radiation

Benedetti measured the anaerobic carbon dioxide production by yeast following exposure to a high-frequency electro-magnetic field. Either increases or decreases in fermentation rate were found, depending upon the culture medium, the duration of treatment and the frequency used. Others have claimed that the fermentative rates and capacities of a number of yeasts, molds and bacteria were markedly increased by electromagnetic radiation of wavelengths between 1.8 millimeters and 120 meters (168). Stimulation of carbon dioxide production by yeast after exposure to radiation of wavelengths 1.7 and 1.88 meters has also been reported (237). Claim of stimulation of bacterial fermentation is made in a patent issued to Ternion A.-G. (294).

MECHANISM OF THE EFFECT OF RADIATION ON RESPIRATION

As to the mechanism by which the respiration rate is influenced by radiation relatively little definitive information is available. Respiration is the expression of a congeries of delicately balanced processes and hence is exceedingly sensitive to internal and environmental conditions. It seems altogether probable that no single explanation will be found for the effects observed in widely diverse types of living material and produced by various kinds of radiation. In many instances the effect upon respiration is doubtless a secondary result of some other process or processes which are more directly influenced by the irradiation. This would appear to be especially true of non-visible radiation.

The influence of radiation upon respiration and fermentation of yeast has been shown, in some instances at least, to be of an indirect nature. Stimulation could be induced in non-treated suspensions by addition of the cell-free culture fluid from ultra-violet irradiated suspensions and, to a lesser degree, even by addition of culture medium or of glucose solution which had been rayed in the absence of the yeast. The authors concluded that irradiation of yeast increases the production of a substance (formed also by non-irradiated yeast) which stimulates the respiration (86).

Norris and Ruddy believed that radiation acts by killing a portion of the cells which thereby liberate the stimulatory substance. In the luminous bacterium, *Achromobacter fischeri,* Giese (105) found, however, that extracts from irradiated bacteria or from eggs or

sperm of *Arbacia* had no specific stimulatory effect on the oxygen uptake, but acted merely as nutrients. Numerous studies by other workers also have demonstrated that irradiation of the culture medium alone can have a marked effect upon the growth and metabolism of cells subsequently inoculated into it. The primary action of the radiation seems to be chiefly on the organic constituents, usually carbohydrates, of the medium.

A question which has oftentimes been raised is whether the changes in rate of gas exchange observed to result from irradiation with light have any relation to the normal respiratory processes. In this connection the view has been advanced that the increased absorption of oxygen or emission of carbon dioxide is due to a photochemical reaction entirely unconnected with respiration. In green plants such a photochemical reaction might be bound up with the photosynthetic mechanism (*e.g.*, 95, 98). The depressant effect of high oxygen concentration upon the rate of photosynthesis in intense light has been interpreted by some as evidence of a photoxidation.

It is, of course, well known (*e.g.*, 71, 78, 235) that radiation of various wavelengths promotes chemical transformations, *in vitro,* of many substances which occur in plants. Some of these reactions are accompanied by absorption of oxygen or liberation of carbon dioxide or both. There are many examples also of *in vivo* chemical reactions which are directly or indirectly influenced by radiation. Since, for the most part, such reactions have not been studied in relation to the gaseous exchange of the plant, a discussion of this literature will not be attempted here. On the other hand, the destructive effects (most frequently observed as a bleaching of the chlorophyll) occasioned by exposure of green plants to light of high intensity which have been noted by many workers, have in a number of cases been accompanied by increased oxygen uptake. It appears altogether reasonable then, that photochemical reactions may be directly involved in some of the experiments cited above. Whether any of these instances can be explained entirely on such a basis is uncertain. If this were the case, it might be expected that the amount of excess "respiration" would be related to the amount of photolabile cellular material present. Such a relationship is indeed indicated by the data of Myers and Burr who suggest that photoxidation may depend upon absorption of light by the chlorophyll. Possibly this hypothesis could be tested by a comparison of cells

with different chlorophyll contents or by a comparison of wavelengths absorbed to different degrees by chlorophyll; the influence of added sugar or of other respirable materials on the light effect might be worthy of investigation also. Other results (91) mentioned above, indicated that greater photoxidation effects were obtainable with sugar-enriched leaves, but the experimental material employed appears to have been unfavorable for quantitative studies.

A photochemical reaction which conceivably may be of widespread occurrence is nitrate reduction (173a, 316). As oxygen is produced in this case the result would be a diminution of the apparent respiration (as measured by oxygen consumption) in light. There is fairly general agreement that the reduction of nitrates by green plants is enhanced by irradiation, a circumstance which may be of significance in this connection, although it is not established that the effect is direct.

Of considerable interest with regard to the mechanism involved is the oft-repeated observation of a respiratory effect in darkness following irradiation. Obviously, the overall reaction can not strictly be termed photochemical, inasmuch as it persists long after absorption of radiant energy has ceased. It is to be regarded, rather, as a complex process in which some primary photochemical step, often requiring a relatively small amount of energy, sets in motion a long-continuing train of events.

Turning now to the possible effects of radiation upon the respiratory mechanism itself, it is well known that the activities of many enzymes[5] are influenced profoundly by diverse forms of radiation. The activities of *in vitro* preparations are usually diminished particularly by γ-rays, x-rays and ultra-violet (for literature see 78, 218, 235, 264, 326). Some coenzymes, too, have been found to be destroyed by ultra-violet irradiation (*e.g.*, 309, 315).

Several examples of enzyme inactivation by visible radiation have been reported: *e.g.*, catalase (171, 172, 220, 331), peroxidase (137), succinodehydrogenase (236), yellow enzyme (295), sucrase (72, 137, 139), diastase (109, 213).

On the other hand, numerous investigators have noted increased activity of enzyme preparations following exposure to visible radia-

[5] No distinction is made here between preparations containing only the enzyme and systems in which the substrate also is present. A number of workers have shown, however, that the effects of irradiation may differ in the two cases.

tion: *e.g.,* catalase (58, 149, 206, 207), peroxidase (14, 220), xanthine oxidase (16), various dehydrogenases (161, 163, 171, 306), amylase (56, 58, 109, 134, 203, 207, 210, 213), sucrase (107, 108, 201, 207, 209, 210), pepsin (56, 149), trypsin (149), papain (18), proteases (58, 202, 209, 210), lipase (58, 149, 204, 209, 223), urease (205). In a few instances ultra-violet, infra-red or x-ray irradiation also has been found to increase enzyme activity *in vitro.*

A special case of light activation is that produced by polarized light (9a 9b, 181a, 267a). Others have been unable to confirm this finding (47a, 143a, 213).

As has been pointed out by numerous investigators, conclusions from *in vitro* studies should be applied only with the greatest reserve to *in vivo* reactions. Experiments relating to alterations of enzyme activity of plants following irradiation *in vivo* are less numerous. Green found an increase of diastatic activity when living leaves were exposed to infra-red, red or blue radiation and concluded that the treatment promoted the conversion of a zymogen into the active enzyme. Others found a 30% decrease in the catalase activity of yeast which had been exposed to sunlight for 30 minutes (308), and later that irradiation by a quartz mercury arc resulted in two- to eight-fold increases in the catalase activity (307). Abramov also noted augmented catalase activity of yeast after exposure to ultra-violet radiation, whereas sucrase, zymase, maltase and proteolytic enzymes were inactivated in various degrees. Yamafuji observed increases in catalase activity up to 2,400% after exposure of various yeasts to radiation from a quartz mercury arc. The effect was due chiefly to the shorter ultra-violet region. The increased acidity following illumination of the light-sensitive seeds of *Nicotiana tabacum* and *Verbascum thapsus* was interpreted as evidence of enhanced lipolytic activity (99). Burge and Burge, who transferred *Spirogyra porticalis* from a frozen lake to higher temperatures, observed a more rapid increase of catalase activity if the plants were illuminated.

Illuminated detached leaves of *Allium tuberosum* and of *Mangifera indica* were observed to have a greater catalase activity than those which had been kept in darkness (246). Similar results were obtained with *Croton* leaves (242). If sugar were supplied to the leaves, however, no difference in enzyme activity was found. These

results were believed to indicate a relationship between hexose production and the catalase activity of the leaf. Catalase and peroxidase activities of rice seeds were diminished by exposure to sunlight (155), whereas no significant difference in catalase activities of *Raphanus sativa* seedlings germinated in dark or in light was noted (60). Ascorbic acid oxidase activity was less in seedlings germinated in sunlight than in those developed in darkness (212), and when soaked seeds of tau-sagyz were exposed to radiation from a quartz mercury arc and the catalase activity of the seedlings measured after two days of germination, the treatment resulted in increases up to 16-fold.

Fuller subjected bean and tomato plants to successive short daily exposures to ultra-violet radiation sufficient to cause serious injury. At the end of seven days of treatment the amylase, invertase, peptase and catalase activities, on a fresh weight basis, were markedly higher in the irradiated plants than in the controls. Slight increases in the activity of amlyase and peptase were observed also in mycelia of *Fusarium lini* which had received ultra-violet irradiation just sufficient to kill. Other investigators have noted increased enzymatic activity attendant upon the killing of plant tissues by ultra-violet irradiation, but these responses do not appear to be specific, since many other methods of causing death have the same result.

Harker reported decreased invertase activity of yeast following exposure to γ-radiation (plus some β-radiation) from radium.

The remarkable reports of increased diastase activity in corn and potato plants days or even weeks after exposure of the seeds and tubers to visible or infra-red radiation (274), are difficult to evaluate, since neither the development of the plants nor the transmissions of the filters employed were described.

In only a few of these studies has respiration been measured along with enzyme activity. Although the rôle played in plant respiration by the known oxidation-reduction enzymes and by the carbohydrases is at present very imperfectly understood, it does not seem unreasonable to expect that changes in the activities of such enzymes might be reflected in an altered gaseous exchange. Giese concluded that the decline in rate of oxygen consumption, observed by him to follow ultra-violet irradiation of *Achromobacter fischeri,* could be interpreted best as due to a decrease in the concentration of dehydrogenases (105).

In the experiments in which attempts have been made to correlate the effects of radiation upon respiration and on enzyme activity of the plant, it has usually not been possible to demonstrate a close relationship. Von Euler and Laurin, who noted a 30% decrease in catalase activity as the result of solar irradiation of yeast, found at the same time only a 5% reduction in fermentation capacity.

Ranjan and Mallik observed that catalase activity, found to be influenced by illumination, was not consistently correlated with the respiration rate. In wheat plants, also, the respiration rate was not correlated with the catalase activity, which was increased by low temperature storage in darkness but decreased by similar storage in light (70). Schröppel reported that the increase in respiration rate resulting from illumination of light-sensitive tobacco seeds preceded by some hours the increases in catalase and peroxidase activities. Pal apparently observed an increase in the value of the respiratory quotient on illumination of germinating *Helianthus* seeds and concluded that light decreased the rate of conversion of fat to carbohydrate (224). The same conclusion was reached by Brown.

Some experiments concerning oxidase activities of plants following ultra-violet irradiation (325) have been mentioned in a preceding section. Regrettably, interpretation of these experiments is rendered difficult by the failure of the authors to specify the basis on which the enzyme activities were compared or to present information which would permit an assessment of the rôle played by the radiation injuries encountered. From the data presented, however, the activity of none of the enzymes studied appears to be quantitatively correlated with the respiration rate.

Petry was unable to detect any effect on catalase or peroxidase activity of legume seedlings which had been x-rayed under conditions presumably identical with those which resulted in a 10% decrease in respiration. In seedlings of *Helianthus annuus* from x-irradiated seeds, the rate of carbon dioxide evolution and the catalase activity were decreased, while the oxidase activity was unaffected (142).

Among the less direct mechanisms through which the respiration rate could conceivably be affected by radiation may be mentioned those which influence (*a*) the amount of available respiratory sub-

strate and (*b*) the rate of movement of materials in the plant or the exchange between plant and environment.

In 1876 Borodin suggested, as have also a number of later investigators, that the observed stimulations were due to increased concentration of respiratory substrate made available by photosynthesis during the illumination period. This appears to be a likely explanation of some of the findings noted, although direct proof is lacking. On the other hand, such an explanation would not seem to apply, without some modification, to the results of Palladin, who measured the carbon dioxide production of leaves detached from etiolated *Vicia faba* seedlings and floated on sucrose solutions. The respiration rate in darkness after a few days of exposure to daylight was more than twice as great as that of leaves which had been maintained continuously in the dark. Increased respiration was noted also after sojourn in blue or in yellow light. No consistent difference between the results obtained with the two spectral regions could be established; no effort to equalize the intensities seems to have been made, however. Possibly an intensity difference accounts for the greater stimulation produced by white light than by the colored light.

The above explanation based on substrate accumulation due to photosynthesis is also not supported by experiments with *Hormidium* and *Oocystis* (303). Respiratory stimulations of approximately the same degree were found consistently after periods of illumination, whether the carbon dioxide concentration was high or was kept at a very low level by the presence of potassium hydroxide. Parija and Saran found respiratory increases following brief illumination of detached leaves shown to be incapable of appreciable assimilation. In other experiments, too, there was noted a respiratory stimulation after exposure, even though the rate of photosynthesis was not great enough to overbalance the carbon dioxide excretion (241, I). Furthermore, as pointed out, for example, by Stålfelt (281), a decrease in concentration of photosynthate rapid enough to account for the frequently observed swift decline in respiration rate subsequent to illumination would also require explanation.

In addition to the possible rôle of photosynthesis in increasing the amount of respiratory substrate, enzymes such as diastase and invertase, of which the activity has been shown to be influenced by radiation, are doubtless important in determining the concentration

of respirable materials in the cell. A diurnal periodicity in invertase activity of tobacco plants, manifested by a high synthetic activity during the day and a high hydrolytic activity at night, has been reported (289). In one of the two varieties studied the respiration rate also showed a maximum during the day and a minimum at night. Daily periodicity of respiration and of enzyme activity in plants has been noted frequently; however, light may not be the factor which governs this phenomenon (see *e.g.,* 124, 256).

Although there has accumulated considerable evidence that secondary carbohydrate transformations in plants may be influenced by radiation, such effects have usually not been shown to be related to the respiratory process. A notable exception is the demonstration that brief illumination of starved detached *Aralia* leaves resulted both in marked stimulation of the subsequent dark respiration and in two- to seven-fold increases of the reducing sugar content (227). Preliminary experiments by the writer with other species of plants appear to confirm these findings. No change in reducing sugar content during exposure to ultra-violet radiation was found by Ranjan (243).

Reference should be made at this point also to the special metabolism of succulent plants. (For literature see 13, 84, 323a.) These plants exhibit a diurnal cycle of accumulation and disappearance of organic acids correlated with fluctuations of the respiratory quotient. During the night the acid content rises, while the R.Q. falls, sometimes to very low values; during the day the situation is reversed. This periodicity is correlated with the natural periods of darkness and light, and some investigators (*e.g.,* 251, 279), have ascribed the deacidification and concomitant carbon dioxide production primarily to a photolytic reaction. However, other factors, especially temperature, are also very important, so that the specific rôle of light seems to be far from clear as yet.

The availability of substrates for respiration conceivably could be determined also by the inter- and intra-cellular permeability. Numerous experimental observations have been interpreted as demonstrating that radiation increases the permeability of plant cells to a variety of substances (20, 36–38, 41, 42, 44, 130, 133, 138, 145, 146, 164-167, 170, 178, 190, 217, 234, 240, 257, 267, 290, 297-299, 311, 320, 321). Under other conditions radiation has been claimed to be without effect or even to cause a decreased permeability (31, 39,

40, 131, 132, 147, 251, 257, 258, 304, 332). Unfortunately, the term permeability as used by various authors has doubtless included many distinct physiological phenomena. It seems not unlikely that the apparent influence of light on some of these is in reality the result of a respiration response rather than its cause.

The rate of transport of respiratory materials within the plant or within the cell also might be of importance in regulating the respiration rate. Protoplasmic streaming, or cyclosis, which no doubt plays a significant rôle in such transport, is intimately related to radiation. (For literature see 32.) In this connection it should be mentioned, however, that certain studies suggest that cyclosis may be controlled by respiration rather than the reverse (75, 287, 288, 296).

There exists, in addition, some evidence that growth-promoting substances, or auxins, may, under certain conditions at least, exert an effect upon plant respiration. Since the activity of auxin in the plant is known to be influenced by radiation, a conceivable mechanism might consist of the chain: radiation-auxin activity-respiration. Sufficient information to permit an evaluation of this possibility is not yet available.

Since respiration is commonly measured by gaseous exchange, it is obvious that factors which influence the rate of gas exchange even indirectly also affect the apparent respiration. For example, it has long been known that the gaseous exchange of many leaves is, to some extent, controlled by the degree of stomatal opening which is in turn closely dependent upon illumination conditions. Alterations in permeability or of other physical properties of protoplasm, such as viscosity, which might regulate diffusion rates, could play a rôle in this way too.

Other properties such as electrical charges and potentials of tissues, the pH of the cell sap and oxidation-reduction potentials of cell suspensions also are known to be influenced by radiation, on the one hand, and to be correlated with respiration processes, on the other. So little is as yet understood, however, of the cause and effect relationships which link these properties and processes that an extended discussion would not appear particularly profitable at the present time.

Finally, mention should be made of another phenomenon which appears to the writer potentially capable of playing a rôle in the observed effect of radiation on respiration in certain instances.

There is accumulating, from many types of experiments, evidence that certain plant cells possess a mechanism for storing carbon dioxide which can be released later (see *e.g.* 276, 277). If this release is influenced by radiation, as is indicated by other work (83), it might furnish an adequate explanation of some of the findings described above. Such a mechanism would appear to have, at most, only an indirect connection with the true respiration. (See also 171a.)

Emerson and Lewis, using the Warburg manometric technic, observed that illumination (by a sodium lamp at intensities slightly below the compensation point) of a suspension of *Chlorella pyrenoidosa* was followed by a large but short-lived effect on the rate of pressure change, which could be attributed to a production of carbon dioxide unaccompanied by a corresponding absorption of oxygen. The maximum rate of this carbon dioxide evolution, which under certain conditions amounted to several times the rate in the preceding dark period, was usually attained within a minute. The rate then fell rapidly to about the level of the dark value, and after passing through a much smaller second maximum exhibited a gradual decrease with time. On darkening the culture a reverse phenomenon resulted, namely, a transient uptake of carbon dioxide, of which the maximum rate was, however, much smaller than that of the evolution in light. Within a few minutes carbon dioxide began to be liberated, the rate increasing continuously over a period of several minutes. The rate of oxygen consumption exhibited only a small (perhaps insignificant) maximum, concurrent with the carbon dioxide burst in light and showed no anomaly when the suspension was darkened.

The amount of the extra carbon dioxide produced in light, beyond that equivalent to the oxygen consumed, was calculated to be of the same order of magnitude as the extra amount absorbed on darkening. This correspondence suggests the presence in the plant of some sort of reservoir of carbon dioxide which tends to empty itself on illumination and to become refilled in darkness. The effect was demonstrated to be connected with the vital activity of the organism, since boiled cells failed to show the response. Concentrations of phenylurethane which completely inhibited photosynthesis also suppressed the activity of the reservoir. In a concentration of 0.005% urethane, photosynthesis was reduced by 50%, but

the initial carbon dioxide burst was unaffected, whereas the second slower phase of carbon dioxide production was completely inhibited. This finding suggests that the two phases of carbon dioxide evolution represent distinct processes. Franck has attempted to explain the phenomenon as a special case of the normal induction period of photosynthesis (90).

The characteristics of the carbon dioxide burst were found by Emerson and Lewis to depend upon a number of conditions. The amount of carbon dioxide evolved increased with the light intensity. Initial exposure to a low intensity only partially emptied the reservoir, and subsequent increase in intensity then produced a new burst of carbon dioxide. Maximal effects were obtained at intensities considerably below those required to saturate photosynthesis. Since the filling of the reservoir in darkness is a slow process (requiring several hours for completion), maximal light effects were obtained only after long dark periods. The amount of carbon dioxide absorbed by the reservoir is determined by the partial pressure of carbon dioxide in the environment. At carbon dioxide concentrations below about 0.5% only small bursts were noted in light. Large bursts were found at 5% carbon dioxide and still larger at 12%. The upper limit was not determined.

Both the filling and emptying of the reservoir are dependent upon temperature. At lower temperatures the bursts are smaller and less rapidly completed. The composition of the culture medium, especially with regard to the micronutrients, also was stated to exert an influence on the behavior of the reservoir.

SUMMARY

A review of the literature supports the conclusion that, under some conditions, an increase of the rate of "apparent" respiration, as measured by gaseous exchange, may be induced by irradiation of various species of plants and types of plant tissues. In the present elementary state of our knowledge it can not be decided with certainty whether or not the observed stimulations are directly related to the "true" respiration. Despite the long-continued interest in this problem the results thus far available are almost entirely of a descriptive nature, and in no single case has there been presented, as yet, a satisfactory elucidation of the mechanism involved. From a consideration of the diverse conditions and types of material with

which an alteration of the gaseous exchange has been observed, it seems altogether likely, however, that such an effect may be the common end result produced by a variety of phenomena.

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Endomitosis	A. Lorz *Seton Hall College*
Tropical Fruits and Their Future	S. J. Lynch *Sub-tropical Experiment Station*
Paleobotanical Taxonomy	H. L. Mason *University of California*
Cell-shape	E. B. Matzke *Columbia University*
Plant Disease Introduction	W. A. McCubbin *Bureau of Entomology and Plant Quarantine*
Plant Oils	J. B. McNair *Field Museum, Chicago*
Genetics and Cytology of Forage Grasses	W. M. Myers *Pennsylvania State College*
Recent Advances in the Science and Technique of Seed Analysis	R. H. Porter *Iowa State College*
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Distribution and Composition of Paleozoic Floras in North America	C. R. Read *U. S. Geological Survey*
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Taxonomy of North American Fresh-Water Algae	L. H. Tiffany *Northwestern University*
Nematode Diseases of Plants	A. L. Taylor *Bureau of Plant Industry*
Measurement of Soil Moisture	F. J. Veihmeyer *University of California*
Control of Fungi in Lumber during Air-Seasoning	A. F. Verrall
Utilization of Native Plants by the American Indians	P. A. Vestal *Harvard University*
The St. Lawrence River as a Biological Habitat for Higher Plants	Fr. Marie-Victorin *University of Montreal*
Vegetable Seed Treatment	J. C. Walker *University of Wisconsin*
Modern Views and Facts About Growth Substances	P. W. Zimmerman *Boyce Thompson Institute for Plant Research*

Proposed Future Contents of
THE BOTANICAL REVIEW

Articles received and awaiting publication

Plant Microfossils	L. R. WILSON *Coe College*
Heterosis	W. G. WHALEY *Barnard College*
Antibiotic Substances Derived from Micro-organisms	J. C. HOOGERHEIDE *Corsan Research Laboratories*

Articles arranged for most recently

Heart Rots in Living Trees	R. W. DAVIDSON *Bureau of Plant Industry*
Destructive Foreign Plant Diseases not known to be established in North America	N. REX HUNT *Bureau of Entomology and Plant Quarantine*
Detached Leaf Culture	C. E. YARWOOD *University of California*

Articles in course of preparation

The Cytology of Fertilization in Angiosperms	L. E. ANDERSON *Duke University*
Development of the Madro-Tertiary Flora	D. I. AXELROD *University of California*
Relation of Wood Anatomy to Taxonomy	I. W. BAILEY *Harvard University*
Anthocyanin Pigments	F. BLANK *Switzerland*
The Genetics of Pollen Tube Growth	J. T. BUCHHOLZ *University of Illinois*
Sexuality and Genetics of Algae	H. BOLD and W. G. WHALEY *Columbia University*
Role of the Endosperm in Seed Development	R. A. BRINK and D. C. COOPER *University of Wisconsin*
The Angiosperm Embryo Sac	EMMA L. FISK *University of Wisconsin*
The Male Gametophyte of Angiosperms	A. GERSHOY *University of Vermont*
Cytogenetics of Nicotiana	T. H. GOODSPEED *University of California*
Tundra Vegetation	R. F. GRIGGS *George Washington University*
American Agar Industry	H. J. HEMM *Duke Marine Laboratory*
Laboratory Testing of Spraying and Dusting Fungicides	J. G. HORSFALL *Connecticut Agriculture Experiment Station*
Cytology and Genetics in Relation to Taxonomy	C. L. HUSKINS *McGill University*
A Critical Survey of the Present Status of Plant Embryology	D. A. JOHANSEN *Stanford University, Cal.*
Techniques for Aseptic Growth of Plants	L. C. KNORR *Cornell University*
Protoplasmic Connections	L. G. LIVINGSTON *Harvard University*

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